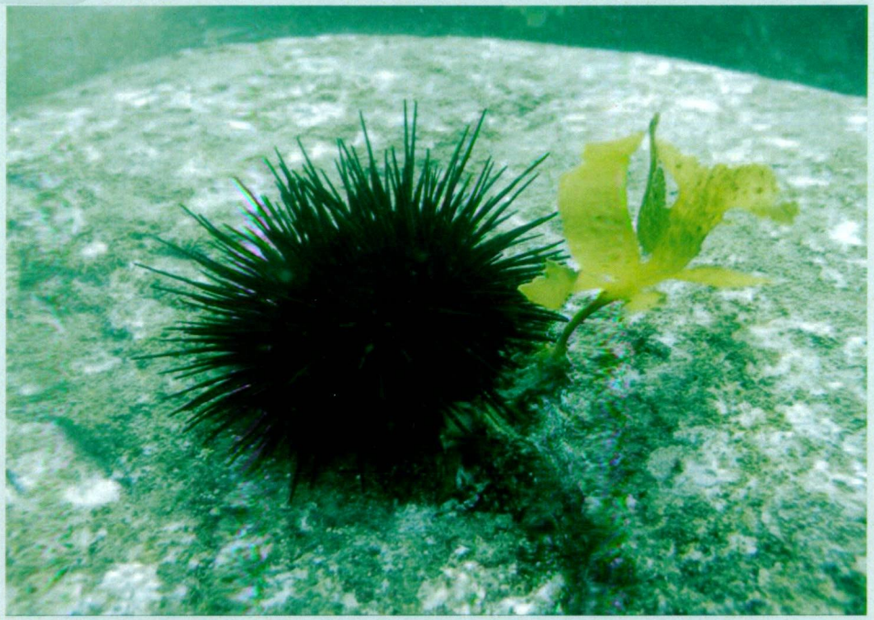
CLIMATE CHANGE AND A RANGE-EXTENDING SEA URCHIN: CATASTROPHIC-SHIFTS AND RESILIENCE IN A TEMPERATE REEF ECOSYSTEM



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CLIMATE CHANGE AND A RANGE-EXTENDING SEA URCHIN S.D. LING

Growing up in Hobart, my intrigue in all things aquatic began at a young age. Completing a BSc Hons (Marine, Freshwater & Antarctic Biology) at the University of Tasmania in 2000, my subtidal research experience includes more than 1000 dives over 10 years in the temperate bioregions of southeastern Australia.

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CLIMATE CHANGE AND A RANGE-EXTENDING SEA URCHIN: CATASTROPHIC-SHIFTS AND RESILIENCE IN A TEMPERATE REEF ECOSYSTEM

BY

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(A joint CSIRO & UTAS PhD program in quantitative marine science)

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University of Tasmania

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CSIRO

UTAS

Declarations

Statement of originality

This thesis contains no material that has been accepted for a degree or diploma by the University or any other institution. The work contained in this thesis, except where otherwise acknowledged, is the result of my own investigations.

Signed:  (Scott Douglas Ling)

Date: 15-6-2009

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Abstract

The barrens-forming sea urchin *Centrostephanus rodgersii* (Diadematidae) has undergone recent poleward range-extension to eastern Tasmania. This thesis examines multiple processes influencing the shift from seaweed beds to sea urchin barrens and integrates the findings within the conceptual framework of catastrophic-shifts between the alternative reef states. This thesis identifies two processes acting to alter this temperate reef system: 1. Climate change - resulting in the poleward migration of a habitat-modifying species; and 2. Fishing - resulting in reduced ecosystem resilience.

Examination of *C. rodgersii* population dynamics across the extension-region reveals that recent warming has led to a coastal regime where sea temperature is now suitable for *C. rodgersii* larval development. Furthermore, the timing of the sea urchins' arrival, age-structure and spatial distribution across the extension-region is consistent with patterns in sea temperature and dispersal potential driven by the EAC. As in the species historic range, *C. rodgersii* in eastern Tasmania is now found in association with barrens habitat; and field experimentation reveals that creation of barrens by this sea urchin results in local biodiversity loss in the order of ~150 taxa that associate with Tasmanian seaweed beds. Furthermore, seaweed-sea urchin dynamics are observed to be broadly consistent with that observed from within the sea urchins' historical range, suggesting that the ecological importance of *C. rodgersii* will be similar across the extension-region.

Field experiments identify the spiny lobster (Palinuridae) as the chief predator of *C. rodgersii* within the extension-region and trials inside/ outside Marine Protected Areas (where size and abundance of lobsters has recovered following cessation of fishing) demonstrate that *C. rodgersii* survival rates are decreased in the presence of large predatory lobsters. Indeed, the predatory interaction between lobsters and *C. rodgersii* is highly size-specific with only lobsters well above the harvested size-limit physically capable of predating on *C. rodgersii*. Importantly, such predatory capable lobsters have been functionally extirpated from much of the Tasmanian coastline due to intensive fishing for well over a century. The culmination of this thesis is that fishing, by removing large predators, equates to a reduction in ecosystem resilience and increased risk of catastrophic-shift in the face of changing climate.

Acknowledgements

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To my co-supervisor Stewart Frusher, thankyou for making available technical and field support (through the Crustacean Section of TAFI) and providing timely feed-back on submitted work. I am very grateful for your "can do" attitude particularly with regard to uncovering behavioural aspects of marine animals using remote video technology. I would like to acknowledge the important role played by Alistair Hobday who helped broaden my thinking on larger-scale ecological processes. I also thank Ken Ridgway for assistance in extracting long-term oceanographic trends in eastern Tasmania; Malcolm Haddon for assistance with modelling sea urchin growth; Arthur Ritar, Mark Grubert, and Alan Beech for providing equipment and laboratory space within the TAFI aquaculture facility; David Mills for assistance with tag-recapture modeling and deployment of video monitoring equipment; and Graham Edgar for assistance in identifying invertebrate fauna.

The large field effort demanded by this thesis would not have been possible without the assistance of many divers and surface attendants who frequently withstood challenging conditions thrown up by the exposed Tasmanian coast. Particular acknowledgment goes to Anthony Reid, Dave Stevenson, Luisa Lyall, Simon Talbot, Adam Stephens, Richard Holmes, Shane Fava, Pip Cohen, Dane Jones, Robbie Kilpatrick, Ryan Downie, Rick Stuart-Smith, Jemina Stuart-Smith, Beth Strain and Regina Magierowski for their assistance with fieldwork and urchin dissections. I also thank the laboratory staff at the School of Zoology for technical support and the Heads of School Alastair Richardson and Sue Jones for their support of my candidature. This thesis was improved following much appreciated proofreading by Jemina Stuart-Smith.

I would like to acknowledge the important role of my family in providing me with the opportunity and support to undertake graduate and postgraduate study. I was fortunate to be able to undertake this research in my home state where I received fantastic support from my father Doug, mother Robin and brothers Max and Sam. I thank them for their continual interest and support of my studies and I particularly thank them for making available the family shack at Bicheno as a field base for this research.

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Statement of co-author contributions

Chapters 2-7 of this thesis have been prepared as scientific manuscripts for submission to peer-review journals as identified on the title page of each chapter. In all cases the design and implementation of the research, data analysis, interpretation of results and manuscript preparation was the responsibility of the candidate but was carried out in consultation with supervisors and other specialist contributors. These contributions are outlined for each chapter below.

Chapter 2: Prof. Craig Johnson (primary supervisor, School of Zoology & TAFI - University of Tasmania (UTas)) contributed conceptual and practical knowledge of sea urchin ecology; Dr. Stewart Frusher (co-supervisor, TAFI) contributed conceptual knowledge and his research team to the collection of field data and larval rearing; and Dr. Catherine King (Australian Government Antarctic Division) contributed her knowledge of larval rearing and data from her honours thesis.

Chapter 3: Prof. Craig Johnson contributed conceptual and practical knowledge of rocky reef systems and sea urchin ecology; Ken Ridgway (CSIRO) provided assistance with long-term climate data for eastern Tasmania; Dr. Alistair Hobday (CSIRO & UTas) provided advice on oceanographic methods; Dr. Malcolm Haddon (TAFI) assisted with the development of urchin growth models.

Chapter 4: This manuscript was improved by comments received from Prof. Craig Johnson.

Chapter 5: Prof. Craig Johnson contributed conceptual and practical knowledge on sea urchin ecology and the dynamics of temperate rocky reef systems.

Chapter 6: Prof. Craig Johnson contributed conceptual and practical knowledge on sea urchin ecology and the dynamics of temperate rocky reef systems; Dr. Stewart Frusher contributed conceptual knowledge of fisheries dynamics, and made available fisheries data and video camera equipment.

Chapter 7: Prof. Craig Johnson contributed conceptual and practical knowledge on sea urchin ecology and the dynamics of temperate rocky reef systems; Dr. Stewart Frusher contributed conceptual knowledge of fisheries dynamics and fisheries data. Ken Ridgway provided assistance with long-term climate data for eastern Tasmania.

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CHAPTER 1: GENERAL INTRODUCTION

Globally, the structure and function of ecosystems is becoming increasingly challenged by human activities (e.g. Vitousek et al. 1997). Importantly, ecosystems are rarely perturbed by a single stressor, and the total magnitude of perturbation on an ecosystem is often the result of multiple stressors acting synergistically (e.g. Beisner et al. 2003). Indeed, the modern context for marine ecosystems involves climate change (*reviewed by* Meehl et al. 2007), intense levels of fishing pressure (e.g. Jackson et al. 2001; Pitcher et al. 2001; Myers & Worm 2003), habitat loss (e.g. Pandolfi et al. 2003; Pyke 2004), invasive species (e.g. Carlton & Geller 1993; Lodge 1993) and pollutants (e.g. Fleeger et al. 2003; Islam & Tanaka 2004). With an increasing intensity and frequency of multiple stressors there is unprecedented risk of dramatic shifts in the structure and function of coastal ecosystems (e.g. Dayton et al. 1998; Jackson et al. 2001; Scheffer et al. 2005; Harley et al. 2006). Hence, there is an urgent need for ecologists to understand ecosystem properties in order to curb trajectories of major ecosystem change and loss of important ecosystem services (e.g. Folke et al. 2004; Hughes et al. 2005).

Sea urchin barrens

One of the most widespread and dramatic ecosystem shifts observed on shallow temperate reefs is the transition from productive seaweed beds to an impoverished 'barrens' state as a result of overgrazing by sea urchins (*reviewed by* Lawrence 1975; Chapman & Johnson 1990; Pinnegar et al. 2000; Tegner & Dayton 2000; Steneck et al. 2002). Indeed, isolating the exact mechanism(s) underpinning this shift has long engaged marine ecologists and has long been demanded by natural resource managers. While few generalities can be made across systems, a frequent conclusion from the literature is that over-harvesting of sea urchin predators results in predatory release and subsequent formation of sea urchin barrens, i.e. that these systems are subject to 'top-down' consumer control (*reviewed by* Steneck 1998; Pinnegar et al. 2000; Tegner & Dayton 2000; Steneck et al. 2002; Halpern et al. 2006). However, many marine systems, particularly when observed at large spatial scales, appear strongly influenced by 'bottom-up' resource effects that are driven largely by physical processes (e.g. Hart & Schiebling 1988; Dayton & Tegner 1984; Dayton et al. 1992; Ware & Thomson 2005; Greene & Pershing 2007). While the mechanisms and dynamics of the transition from seaweed beds to sea urchin barrens appear complex and may be peculiar to particular systems, much of the discussion about shifts between these alternative states has largely occurred within the context of either 'top-down' or 'bottom-up' processes.

Paradigms of temperate reef ecosystems

Traditionally, the research approach in marine ecology has been to frame hypotheses within either the 'top-down' or 'bottom-up' paradigms, collect data at a particular site or spatial scale, and to then interpret the data to either support or reject the hypothesis. The reputation of the 'competing paradigms' is then seemingly established by the relative number of published studies demonstrating either 'positive' or 'negative' results (*see* Menge 2000). Hypotheses framed within the 'top-down' paradigm typically rely on a steady 'equilibrated' ecosystem state, and are generally conducted at local scales amenable to experimental manipulation (*reviewed by* Menge 2000). While investigation of 'bottom-up' control has generally been conducted at larger spatial

scales, on systems with dynamics that are more non-equilibrial in nature, and with heavy reliance on correlative evidence typical of oceanographic studies (e.g. Dayton & Tegner 1984; Dayton et al. 1999; Ware & Thomson 2005; Greene & Pershing 2007; *but see* Worm et al. 2000). These discrepancies in focus and scale have undoubtedly led to a false dichotomy regarding processes structuring marine ecosystems. Thus, the emerging trend toward studies that search for generality across a range of spatial and temporal scales (e.g. Estes & Duggins 1995; Menge et al. 2003; Frank et al. 2006), or which examine the relative strengths of 'top-down' versus 'bottom-up' processes (e.g. Halpern et al. 2006) is refreshing. Interdisciplinary studies, by considering multiple processes at multiple spatial and temporal scales, offer new insights by examining where and when particular processes are important in marine systems, rather than posing the issue as an 'either/ or' question (e.g. Menge et al. 2003; Lotze et al. 2001; Frank et al. 2006; Hunt & McKinnell 2006; Litzow & Ciannelli 2007).

Resilience of temperate reef ecosystems

The transition between the alternative seaweed dominated and sea urchin 'barrens' states appears to be influenced by many processes operating across a wide spectrum of spatial and temporal scales. This includes oceanic processes affecting dispersal, larval development and settlement of urchins from the plankton (e.g. Ebert & Russell 1988; Hart & Schiebling 1988; Wing et al. 2003); habitat preferences (e.g. Andrew 1993); storm events (e.g. Ebeling et al. 1985; Andrew 1991; Dayton et al. 1992; Tegner et al. 1997); effects of sweeping macroalgae (e.g. Konar 2000; Konar & Estes 2003); predation (e.g. Estes & Duggins 1995; Tegner & Levin 1983; Babcock et al. 1999; Shears & Babcock 2002); and disease cycles (e.g. Lessios et al. 1984; Scheilbling & Hennigar 1997; *reviewed by* Steneck et al. 2002; *also see* Lafferty 2004). Thus, temperate rocky reef assemblages are clearly complex and dynamic systems typified by high variability and shaped by interactions between physical and biological processes acting across multiple scales (e.g. Dayton et al. 1998; Tegner & Dayton 2000; Steneck et al. 2002; Micheli et al. 2005).

While such variability typifies marine systems, major perturbations appear capable of pushing ecosystem dynamics beyond the normal range of variability leading to "catastrophic shifts" in structure and function, whereby the underlying dynamic shifts to an alternative domain of attraction with a return to former dynamics difficult once a critical threshold has been passed (e.g. Lewontin 1969; May 1977; Holling 1973; Sutherland 1974; *reviewed by* Scheffer et al. 2001; Beisner et al. 2003; *see* Figure 1a&b). This model is not constrained by traditional paradigms of either 'top-down' or 'bottom-up' control, but encompasses multiple processes at larger spatial and temporal scales and incorporates the role of history, resilience and non-equilibrial dynamics in the tempo and mode of ecosystem change (Hughes et al. 2005; Scheffer et al. 2005). By capturing the uncertain nature of ecosystem dynamics within broad "domains of attraction", this conceptual view moves beyond the typecasting of ecosystems into highly mechanistic 'boxes' that are, by definition, devoid of uncertainty. Indeed, the flagship process typifying the uncertain nature of ecosystems is global climate change, which is forcing a major rethink of processes structuring ecosystems particularly processes based on steady state equilibriums, such as predator-prey cycles (*see* Hughes et al. 2005; Scheffer et al. 2005). This thesis examines multiple processes influencing

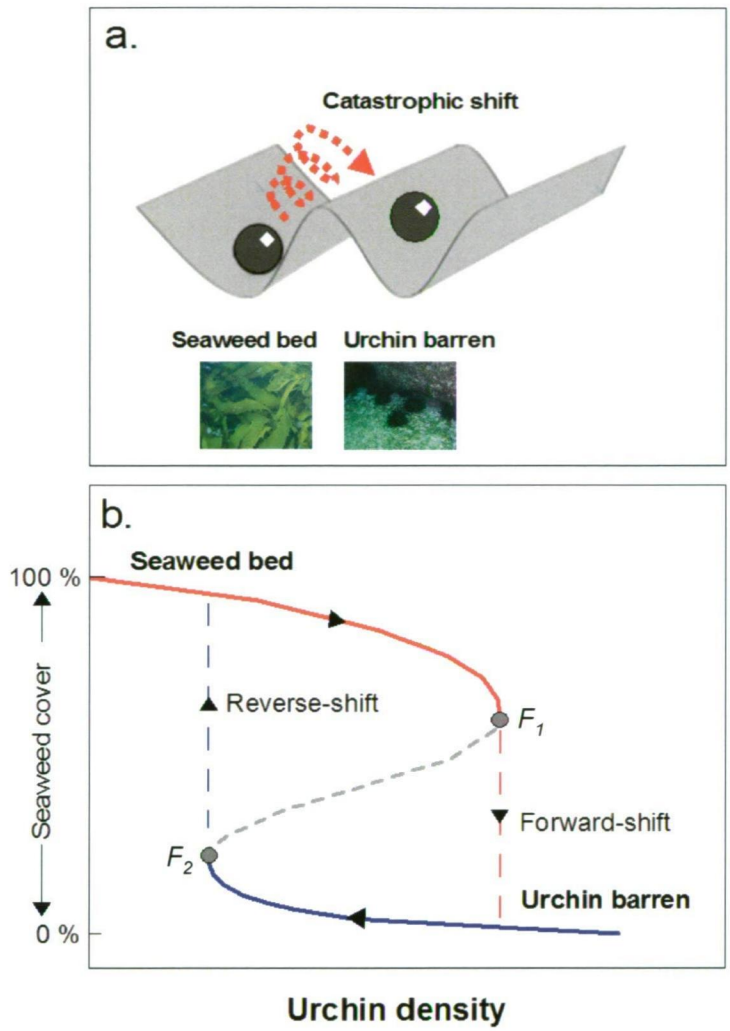

Figure 1. Schematic of catastrophic ecosystem shift between alternative seaweed bed and sea urchin barren states. (a) Corrugated surface whereby valleys represent the respective domains of attraction for the seaweed and alternative sea urchin barrens states. The ball bearing represents the current status of the ecosystem. To undergo catastrophic shift to barrens the system must be pushed (i.e. perturbed) sufficiently for the system (i.e. ball bearing) to move into the new domain of attraction. The 'resilience' (*after* Holling 1973) of a particular ecosystem state against perturbation is represented by the valley depth. Hence, both states possess resilience by acting to retain the ball bearing within a valley. (b) Schematic showing a discontinuous phase shift in 2 dimensional phase-space (*sensu* Scheffer et al. 2001). If the system occurs in the seaweed state, i.e. on the upper path (red), but close to the threshold F_1, a slight increase in sea urchin density may induce a catastrophic shift to the alternative and stable barrens state, representing a `forward shift'. Once the barrens state has been formed, reverting back to the seaweed state by following the lower path (blue) is difficult because the system shows hysteresis, i.e. the 'reverse-shift' only occurs if sea urchin density (i.e. grazing rate) is reduced far enough to reach the return threshold at F_2. The broken grey line indicates the region of instability between the alternative states.

the shift from seaweed beds to sea urchin barrens and integrates the findings within the conceptual framework of catastrophic-shifts between alternative states.

The case study

Shifts from productive seaweed beds to sea urchin barrens in eastern Tasmania (south eastern Australia) have followed recent incursion of the sea urchin *Centrostephanus rodgersii* (Diadematidae). Consistent with the fingerprint of climate change (Parmesan & Yohe 2003), long-term change of the East Australian Current (EAC) has resulted in greater poleward (southward) penetration of warm water leading to coastal warming of eastern Tasmania (Ridgway 2007), which corroborates with poleward range extensions of many marine species in this region, including *C. rodgersii* (Edgar 1997). Extending its range from New South Wales (NSW), *C. rodgersii* was first recorded on remote reefs in far north east Tasmanian in the late 1960s, north east Tasmania in 1978, south eastern Tasmania in the mid-1980s (Johnson et al. 2005); and south western Tasmania in 2005 (J. Valentine *pers. obs.*). Since it was first detected in waters of the Tasmanian mainland coast in 1978, the abundance of *C. rodgersii* has increased, the range has moved further south and incipient (~$1\text{-}10^1$ m) and widespread ($10^2\text{-}10^3$ m) barrens habitat now occur in some locations (Johnson et al. 2005).

Such is the impact of *C. rodgersii* that in NSW ~50% of all near-shore rocky-reef exists as urchin barrens as a result of its grazing activity (Andrew & O'Neill 2000). A similar level of barrens habitat arose on reefs in Tasmanian waters in Bass Strait within ~3 decades of the establishment of *C. rodgersii*, and it is estimated (on the basis of reef substratum structure) that barrens could expand to a similar extent in eastern Tasmania (Johnson et al. 2005). The threat of widespread barrens therefore poses major concerns for biodiversity on Tasmanian reefs and for lucrative reef-associated fisheries (worth ~AUS$150 $M.year^{-1}$ before processing) that are dependent on productive seaweed-dominated habitat (Johnson et al. 2005). While widespread barrens currently occur in relatively few places in eastern Tasmania, a major feature of *C. rodgersii* grazing on this coast is the occurrence of small incipient barrens patches ($1\text{-}10^1$ m) within dense and diverse seaweed beds (Johnson et al. 2005), particularly on major headlands. Given continued climate warming in eastern Tasmania and the potential for further positive effects on *C. rodgersii* populations, new and existing barrens patches are poised to form and coalesce into widespread barrens.

The transition from seaweed beds to *C. rodgersii* barrens provides an example of a classic catastrophic-shift between alternative stable states. Indeed, observations from rocky reefs in NSW indicate that *C. rodgersii* barrens have formed and persisted for over 25 years (*reviewed by* Andrew & Byrne 2001). Demonstrating ecological hysteresis, the density of *C. rodgersii* required to overgraze seaweed beds to form sea urchin barrens has been experimentally shown to be greater than that required to maintain barrens (Hill et al. 2003). Indeed, almost all grazing pressure must be removed to enable seaweed beds to recover (Andrew & Underwood 1993; *reviewed by* Andrew & Byrne 2001; Hill et al. 2003). The combined evidence suggests that both seaweed beds and *C. rodgersii* barrens constitute alternative stable states, or separate domains of attraction of the system, and both states possess resilience (*sensu* Holling 1973) against perturbation (Figure 1a&b). Because the majority of rocky reef in eastern Tasmania currently exists in the seaweed dominated state, the aim of the present

research was to understand processes conferring and eroding resilience of the desired seaweed dominated state against catastrophic-shift to the alternative barrens state in the face of range extension by *C. rodgersii*.

Thesis Structure

This thesis examines multiple processes influencing the shift from seaweed beds to sea urchin barrens and integrates the findings within the conceptual framework of catastrophic-shifts between alternative states. The thesis progresses by initially exploring the range extension of *Centrostephanus rodgersii* in eastern Tasmania with respect to the changing climate of this coast. It then documents the consequences of the catastrophic-shift on reef biodiversity, and concludes by investigating the influence of biological processes and the effects of fishing, on the resilience of seaweed beds against barrens formation by *C. rodgersii*. Because the thesis has been prepared as a series of stand-alone manuscripts, repetition of the important contextual information pertained within the **General Introduction** (Chapter 1), has been unavoidable.

Chapters 2 & 3 examine how oceanography influences reproductive and distributional patterns of *Centrostephanus rodgersii* in Tasmania. **Chapter 2** examines evidence for a reproductive cycle in Tasmanian waters, and the effects of temperature on fertilisation success and larval development of the sea urchin under the relatively cool, but warming conditions of eastern Tasmanian coastal waters. Links between a changing physical environment and the range-extension of *C. rodgersii* are further explored in **Chapter 3** where age-structure and spatial distribution of the sea urchin are correlated with oceanographic patterns.

Chapters 4-6 address biotic interactions of *Centrostephanus rodgersii* within the range extension region. **Chapter 4** examines the impact of *C. rodgersii* grazing on rocky-reef biodiversity within the extension-region by using a series of controlled sea urchin removals. **Chapter 5** describes population dynamics of *C. rodgersii* when the sea urchin is associated with alternative seaweed and recently-formed barrens states; the observed dynamics within the extension-region are then compared to well-documented patterns from within the sea urchins' historical range. **Chapter 6** details a suite of experimental manipulations identifying predators of *C. rodgersii* and examines the effect of fishing on the resilience of seaweed beds against the incursion of the ecologically important *C. rodgersii*. In summary, **Chapter 7** provides a general discussion of this collective body of research and confirms the validity of applying "catastrophic-shift" and resilience theory to the transition between alternative seaweed bed and sea urchin barren states.

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CHAPTER 2: REPRODUCTIVE POTENTIAL OF A MARINE ECOSYSTEM ENGINEER AT THE EDGE OF A NEWLY EXPANDED RANGE

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Abstract

Global climate change is leading to re-distribution of marine species and altering ecosystem dynamics. Given recent poleward range extension of the barrens-forming sea urchin *Centrostephanus rodgersii* (Diadematidae) from mainland Australia to Tasmania, there is a need to understand the population dynamics of this ecologically important species in the Tasmanian environment. This paper informs possible population dynamics of *C. rodgersii* in Tasmania by examining its reproductive ecology in this new environment. Reproductive periodicity (gonad index and propensity to spawn) was assessed bimonthly over 18 months at 4 sites in eastern Tasmania spanning ~2 degrees in latitude. At all sites, *C. rodgersii* displayed a strong seasonal cycle in gonad production with major spawning occurring in winter (~August) at minimum annual water temperature. Gametes from Tasmanian *C. rodgersii* were viable as determined by fertilisation and early development trials. However, development to the 2-arm stage at ~3 weeks was strongly dependent on water temperature across the 8-20 °C temperature range, with poor development occurring below 12 °C. The range of temperatures tolerated by Tasmanian *C. rodgersii* larvae was similar to that of larvae from its native New South Wales range, indicating that this species has not undergone an adaptive shift to the cooler Tasmanian environment. There was also no evidence for an adaptive shift in reproductive phenology. Importantly, coastal water temperatures in eastern Tasmania during the peak spawning in August fluctuate about the 12 °C larval development threshold. Recent warming of the eastern Tasmanian coast and further warming predicted by global climate change will result in an environment increasingly favourable for the reproduction and development of *C. rodgersii*.

Introduction

Range extensions provide important opportunities to investigate the underlying mechanisms defining a species distribution (Holt and Keitt 2005; Parmesan et al. 2005). For changes in species ranges to be detectable, range modifications must occur over large spatial scales of 10s to 100s of km, therefore causal mechanisms must also operate over large spatial scales. In the marine environment, global climate change is a mechanism that has already resulted in, and is predicted to further lead to, widespread re-distribution of species ranges (Barry et al. 1995; Fields et al. 1993; Holbrook et al. 1997; Hughes 2000; Walther et al. 2002; Parmesan & Yohe 2003; Beaugrand 2004; Chevaldonné & Lejeusne 2004; Harley et al. 2006; Poloczanska et al. 2007).

Consistent with long-term climate change and species range shifts around the globe during the last ~40 yrs (e.g. Holbrook et al. 1997; McGowan et al. 1998; Sagarin et al. 1999; Zacherl et al. 2003), the temperate coastal environment of eastern Tasmania has undergone warming primarily as a result of increased southward penetration of the East Australian Current (EAC) (Ridgway 2007). While some warmer water species have become regular members of the Tasmanian coastline, some of these species appear sporadically and generally only occur as juveniles (Edgar 1997). Of the new species now present in Tasmania, the Diadematid sea urchin *Centrostephanus rodgersii* (Agassiz) is one of the most conspicuous and ecologically important due to its ability to catastrophically overgraze macroalgal beds and maintain an alternative and stable sea urchin barrens habitat (Fletcher 1987; Andrew & Underwood 1989; Andrew 1991; Andrew 1993; Andrew & Underwood 1993; Hill et al. 2003; S. Ling *submitted manuscript*). Historically, *C. rodgersii* in Australia has been largely restricted to the coast of New South Wales (NSW, *see* Figure 1) where the associated barrens habitat is estimated to constitute ~ 50% of all near-shore reef habitat (Andrew & O'Neill 2000).

Undergoing a poleward range extension, *C. rodgersii* was first recorded in the Kent Group of Islands in the late 1960s; north east Tasmania in 1978; south eastern Tasmania in mid-1980s; and south western Tasmania in 2005 (Figure 1). Since first detected, the sea urchin's abundance has increased and expansive barren areas now occur in some locations (Johnson et al. 2005). The threat of widespread barrens, as found in NSW, poses major concerns for biodiversity on Tasmanian reefs and for reef associated fisheries (worth ~AUS$300 M.year^{-1}) that are dependent on macroalgal habitat (Johnson et al. 2005, Ling 2008). Dartnall (1980) interpreted the discovery of *C. rodgersii* in north eastern Tasmania as perhaps a temporary bulge in the species range limit, stating "We await evidence that this population is reproductively self-maintaining...". A scenario whereby *C. rodgersii* is capable of completing its life cycle within Tasmanian waters is likely to allow for a more rapid population expansion and greater ecological impacts than if Tasmanian populations are only maintained by occasional cohorts of larvae transported south via the EAC (*see* Figure 1). Therefore, information on the reproductive status of this species in eastern Tasmania is vital to the assessment of spread of this organism and the associated ecological consequences for rocky reef ecosystems in Tasmania.

Reproduction of *C. rodgersii* involves dioecious adults that spawn gametes into the water column where fertilisation occurs (King 1992; Huggett et al. 2005). Fertilised eggs rapidly develop into a two-armed planktotrophic larval stage that exists in the water column for ~100 days before settling to reef substratum (Huggett et al. 2005). This feature facilitates long distance dispersal in oceanographic currents, thus it is likely that the southward incursion of *C. rodgersii* in eastern Tasmania has occurred due to increased larval dispersal driven by changes to patterns of the EAC (*see* Ridgway 2007). Within its native distribution, *C. rodgersii* displays a seasonal cycle in gamete production with the major spawning activity occurring in winter (King et al. 1994; Byrne et al. 1998). Given the cooler water temperatures in eastern Tasmania (winter min. ~11 °C) relative to NSW (winter min. ~14 °C), the ability of *C. rodgersii* to develop functional gonads, viable gametes and undergo normal larval development may be compromised in the Tasmanian environment. This paper assesses the reproductive capability of *C. rodgersii* in eastern Tasmania by examining evidence for the existence of a reproductive cycle, its ability to produce functional gametes and to undergo successful larval development.

Materials and Methods

Study sites

Reproduction of *Centrostephanus rodgersii* was investigated at Elephant Rock, St. Helens (41° 14' 56" S; 148° 20' 18" E); The Gulch, Bicheno (41° 52' 29" S; 148° 18' 27" E); Mistaken Cape, Maria Island (42° 38' 34" S; 148° 9' 17" E); and The Lanterns, Tasman Peninsula (43° 8' 19" S; 148° 0' 21" E) (Figure 1). At all sites, *C. rodgersii* was collected from macroalgal habitat by divers at 8 - 15 m depth. Temporal variability in temperature was determined on the sea floor at each site using temperature loggers (Optic Stowaway©® by Onset) fixed at a depth of 9 m.

Determination of reproductive seasonality

Evidence for reproductive periodicity was investigated by tracking mean gonad index (GI) obtained approximately bi-monthly from a sample of 30 adult *C. rodgersii* from each of the 4 sites over an 18 month period from October 2004 to June 2005. Collections were aimed at sea urchins within the size range of 80-110 mm test diameter (TD) to reduce potential size related biases in GI. Sea urchins were dissected fresh and drained of coelomic fluid plus any free-surface water. Gonads were removed and sexed where possible by the unaided eye (unmagnified swab). Sex ratios were generated for each site by summing males and females across sampling times where sex was determinable for all individuals. Sex ratios for each site, and across eastern Tasmania as a whole (summing sexes across all sites), were examined for departure from a 1:1 ratio using Chi-square tests. Drained gonads, test and spines, gut and contents, and the Aristotle's lantern were weighed separately. GI for each individual was expressed as (gonad weight/total body weight)*100 %. To assess the capacity to spawn, on each sampling occasion an additional 10 sea urchins from each site were injected with 4 ml of 0.5 M KCl through the peristomal membrane. The number of individuals artificially induced to spawn were recorded and expressed as a percentage.

The effect of temperature on fertilisation and larval development

The effect of temperature on fertilisation and larval development was assessed under constant laboratory conditions. Thirty sea urchins (TD 80 to 110 mm) were collected from the Tasman Peninsula (southern most site) near the 2005 peak in GI (23-Aug-2005) and held in aquaria overnight at ambient water temperature (12 °C) prior to commencement of experiments. Adults were selected randomly and injected with 4 ml of 0.5 M KCl. Profusely spawning urchins were individually inverted on top of 500 ml glass beakers to collect gametes 'dry' until gamete release slowed (~10–15 mins). Ambient 12 °C, 0.2 µm filtered seawater (FSW) was added carefully to each beaker and the gametes diluted into stock solutions. Eggs from individual females were serially diluted to make stock solutions of approximately 100 eggs.ml^{-1} determined by counting eggs in 1 ml aliquots using a dissecting microscope. The density of sperm in stock solution was standardised by a series of sperm dilutions and haemocytometer counts on sperm inactivated by Lugol iodine. A spectrophotometer was then used to calibrate the absorbance (at 340 nm) of the desired sperm solution to allow delivery of ~500 sperm to 1 egg in each jar which is the optimal sperm to egg ratio in this species (King 1992). Replicate cultures consisted of sperm and eggs from a different male-female pair. The culture system consisted of 70 ml polystyrene jars arranged in 12 columns by 6 rows across an aluminium temperature gradient block that maintained

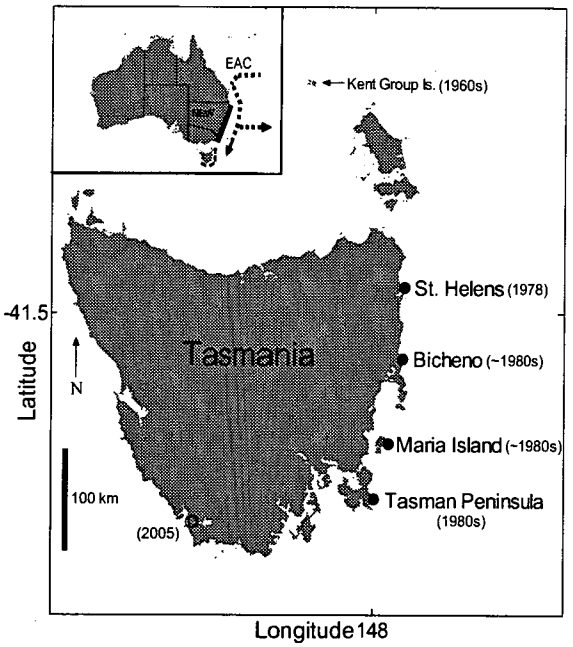

Figure 1. Map of sites used to monitor the reproductive cycle of *Centrostephanus rodgersii* in eastern Tasmania, and the timeline of first sightings. Inset displays mainland Australia and the direction of the East Australian Current (EAC); the 'native' distribution of *C. rodgersii* on mainland (solid line, *after* Andrew & Byrne 2001); and the recent range extension of the sea urchin (broken line, *after* Johnson et al. 2005). The timing of discovery of *C. rodgersii* along the Tasmanian coastline is shown in parentheses (*after* Johnson et al. 2005); the south western range limit is shown as an open circle (J. Valentine *pers.obs.*).

each column at ~8, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, and 20 °C (temperature loggers revealed a constant temperature regime for the entire trial period). The 6 rows in each temperature 'column' allowed 3 replicate gamete sets to be run concurrently. Additional jars containing FSW at each of the test temperatures were also kept on the temperature gradient block to enable isothermal water changes in cultures twice weekly. When functional guts had developed (early pluteus stage, C. King *pers. comm.*), larvae were fed a mixed diet of *Nannochlorpsis oculata*, *Chaetocerus muelleri* and *Isochrysis galbana* (Tahitian strain) at a density of 50,000 cells.ml^{-1} following each water change. Because of the need for intensive sampling during embryonic and early larval development, replicate trials with different gamete sets were commenced 1 day apart.

At the start of each trial, jars were filled with 25 ml of egg solution and equilibrated to the treatment temperatures. An additional 25 ml of isothermal FSW was then added to each jar to obtain a culture density of approximately 50 eggs/ml before addition of 0.01 ml of sperm solution (containing ~1.25x10^6 sperm) with a micropipette. To assess fertilisation rates, 1 ml of eggs was sampled (by taking a random transect across the bottom of the jar) from each temperature treatment 20 mins after the addition of the sperm solution and transferred to 5 ml vials containing 2 ml of 10% formosaline. Fertilisation rate was calculated as the percentage of eggs displaying a fertilisation membrane and the effect of temperature was examined with linear regression using appropriate tests of assumptions. To document development, embryos and larvae were sampled from jars at 2 hrs and at intervals of 30 mins over the first ~4 hrs, and at increasing intervals thereafter. The developmental stage that each culture had reached was assigned as the stage that accounted for > 50% of the embryos/ larvae in the sample. Extractive sampling of cultures was ceased after ~1 day and development was then followed directly in jars using a dissecting microscope (20x). The yield of advanced stage 2-arm plutei for each temperature treatment was calculated as the relative contribution, expressed as a percentage, of the total yield of advanced stage 2-arm plutei from each trial. To assess the possibility of acclimation by *C. rodgersii* to the cooler Tasmanian environment, average development time to the 2-arm plutei stage was taken for each temperature treatment and examined with respect to values for NSW reared larvae (data from King 1992).

Results

Determination of reproductive seasonality

Tasmanian *Centrostephanus rodgersii* produced gonads similar in appearance to those of NSW *C. rodgersii* (C. King *pers.obs.*). The distribution of sexes at each site and for eastern Tasmania as a whole did not deviate significantly from a 1:1 sex ratio (for individual sites minimum P=0.09; for eastern Tasmania as a 'whole', χ^2=1.1, P=0.30). Across all sites, *C. rodgersii* displayed a strong seasonal cycle in gonad production, with major spawning activity occurring in winter (~August) as evidenced by a rapid decline in GI (Figure 2a&2c). The capacity of *C. rodgersii* to undergo induced spawning at each site cycled in a clearly defined pattern with maximal induction of spawning occurring in July-August (Figure 2b). This pattern displayed strong overlap with the timing of the marked decline in GI and was similar at all 4 sites (Figures 2a&2b).

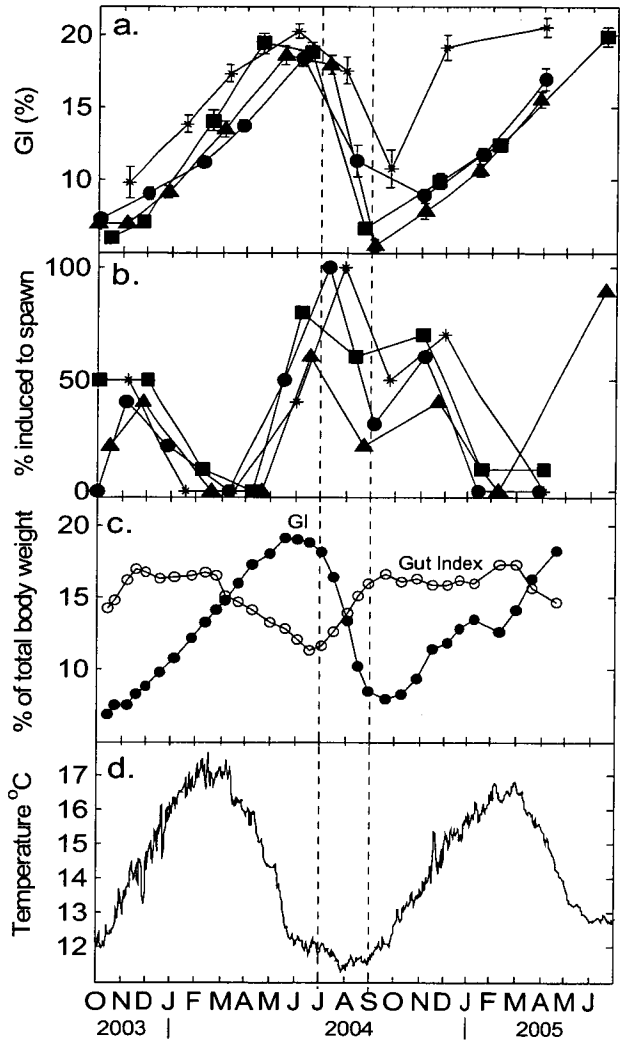

Figure 2. Reproductive cycle of *Centrostephanus rodgersii* at 4 sites in eastern Tasmania, Oct 2003 - Jun 2005. (a) Gonad index, data are means ± SE, n=30. St. Helens *; Tasman Peninsula ▲; Bicheno ●; Maria Is. ■. (b) Capacity of population to spawn, symbols as above. (c) Smoothed cycles of gonad (filled symbols) and gut (open symbols) indices; data represent the running mean calculated on 4 consecutive samples through time. (d) Mean daily temperature on the benthos. Temperature data has been pooled across the 4 monitoring sites (note: data prior to 23-Nov-2004 is daily mean for St. Helens & Bicheno only). Area within the dotted vertical lines indicates the major period of spawning.

The relative decline in GI between gravid (July) and spent states (end of August to early September) was 51 % at St. Helens, 70 % at Bicheno, 60 % at Maria Is. and 70% at Tasman Peninsula. The cycle in GI was the inverse of relative gut weight indicating a normal echinoid pattern of resource acquirement and subsequent transfer of energy to gonad production prior to spawning (Figure 2c). The reproductive cycle of *C. rodgersii* in eastern Tasmania correlated strongly with water temperature. Increasing GI broadly tracked spring-summer periods of increasing water temperature with peak GIs reached during late Autumn and maximum spawning activity occurring during August when water temperatures reached their annual minimum (Figure 2d).

The effect of temperature on fertilisation and larval development

Gametes produced by Tasmanian *C. rodgersii* were viable, with eggs readily fertilised, during the peak winter spawning period. Embryonic and larval development was

normal and the 2-arm pluteus stage was readily reached. While there was a small increase in fertilisation rate with increasing temperature (95-99 % fertilised), variation around this trend was large and so temperature was considered to have little biological effect on fertilisation success over the 8-20 °C range examined (Figure 3). There was however, a strong effect of water temperature on development, with minimal successful development to 2-arm plutei occurring in cultures below 12 °C. Rates of development increased with increasing temperature up to 19 °C, however development rate decreased and became highly variable across replicate trials in the 20 °C treatment (Figure 4). The relative yield of 2-arm plutei across temperature treatments peaked at the mid-range of temperatures tested, i.e. between 14-15 °C (Figure 5). Temperatures below 12 °C did not yield any advanced stage 2-arm plutei (stage 22) and yield similarly declined with temperatures > 16 °C, with very few stage 22 larvae observed in the 20 °C treatment. Indicating a lack of acclimation within the extended range, temperature dependent patterns in development rate were similar for Tasmanian and NSW larvae (Figure 6).

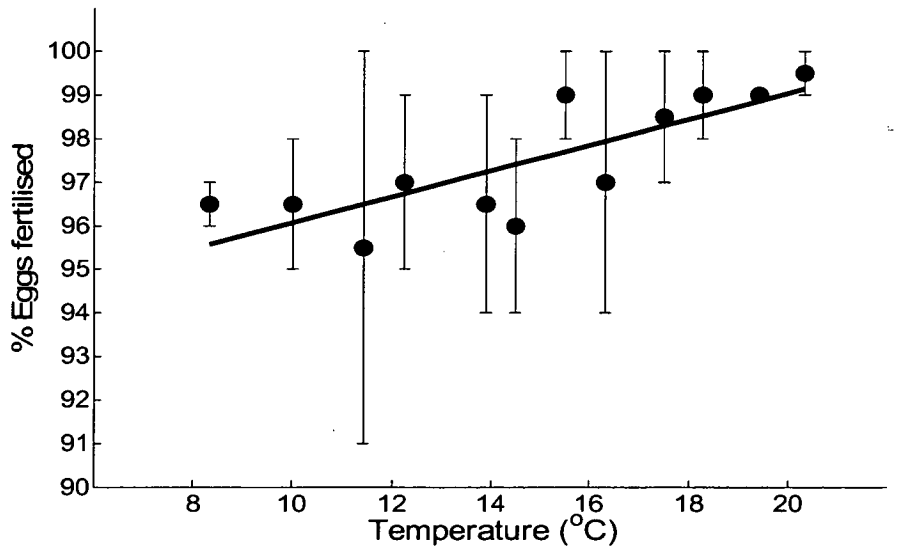

Figure 3. Temperature dependent fertilisation rates of Tasmanian *Centrostephanus rodgersii*. Data are means for 100 randomly selected eggs from 2 replicate trials, ± SE. While linear regression revealed a significant positive trend (treatment: $F_{1,10}$=18.29, P=0.0016), the fit was relatively poor (R^2=0.65) and the size of the effect small ($y = 0.297x + 93.10$).

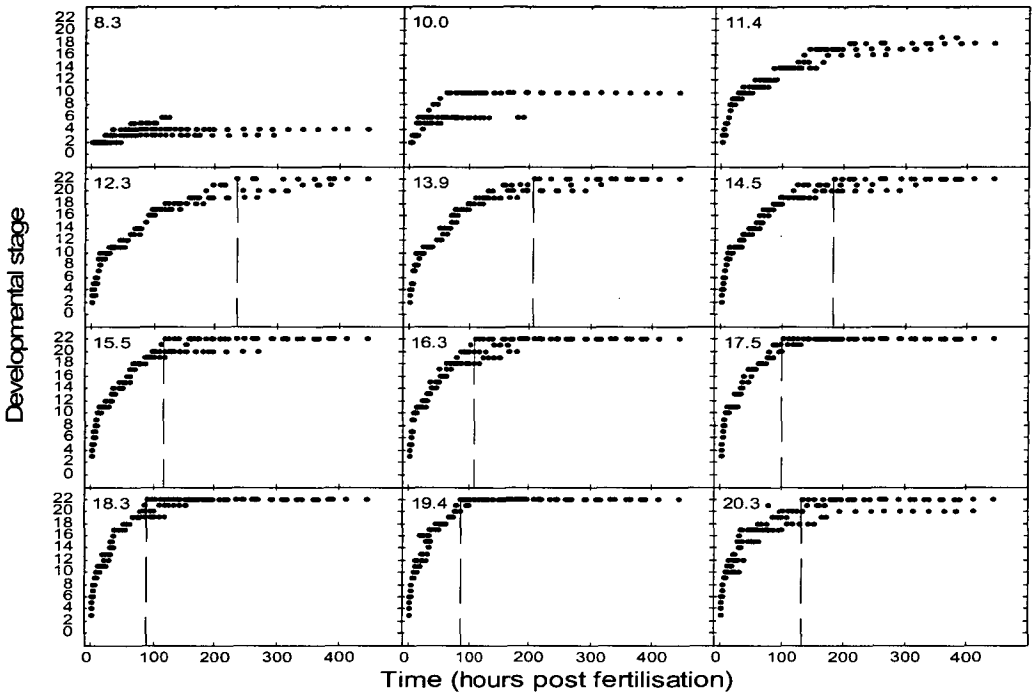

Figure 4. Temperature dependent development rates of Tasmanian *Centrostephanus rodgersii* reared at 8.3 - 20.3 °C. Stages of larval development are (after King 1992): stage 1. unfertilised egg; stage 2. fertilised egg; stage 3. 2-cell embryo; stage 4. 4-cell embryo; stage 5. 8-cell embryo; stage 6. 16-cell embryo; stage 7. 32-cell embryo; stage 8. 64-cell embryo; stage 9. morula; stage 10. early blastula; stage 11. mid-blastula; stage 12. hatched blastula; stage 13. early gastrula; stage 14. mid-gastrula; stage 15. late gastrula; stage 16. early prism; stage 17. mid-prism; stage 18. late prism; stage 19. early pluteus; stage 20. early 2-arm pluteus; stage 21. mid 2-arm pluteus; stage 22. advanced 2-arm pluteus. Broken vertical line indicates the minimum time required to reach the advanced 2-arm pluteus. The advanced 2-arm pluteus stage was not reached in treatments < 12 °C (also not observed up to 35 days [840 hrs] post fertilisation). Rates of larval development increased with increasing temperature up to 19.4 °C, however development rate slowed and became highly variable across replicate trials in the 20.3°C treatment.

Discussion

Reproductive cycle

Seasonal reproductive activity of *Centrostephanus rodgersii* in eastern Tasmania strongly indicates that this sea urchin is capable of completing its life cycle in its new range. Monitoring of gonad indices and spawning capacity over 18 months revealed a similar pattern at 4 sites spanning eastern Tasmania, with a strong seasonal cycle in gonad production and spawning in winter (~August). Maximum population gonad indices (GIs) were recorded in June or July at each site (18.4 – 20.1 %), while minimum population GIs occurred from September to November (5.5 – 9.8 %). The clearly defined spawning period over 1-2 months contrasts the findings of Byrne et al. (1998) within the native range of *C. rodgersii* in NSW, which describe a pattern of increasing spawning period with increasing latitude. Northern NSW populations had a

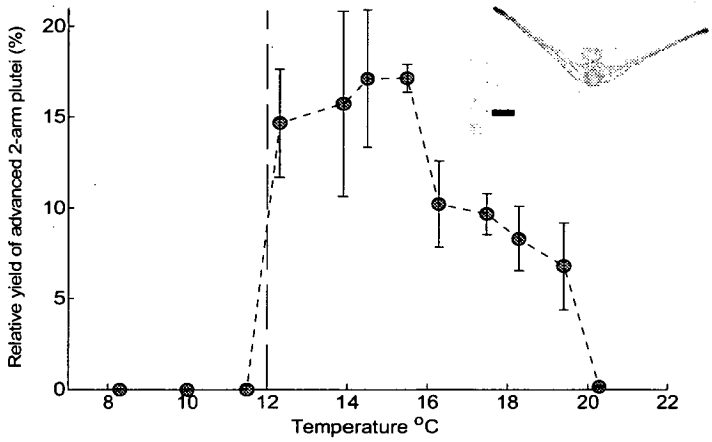

Figure 5. Temperature dependent yield of advanced 2-arm plutei of Tasmanian *Centrostephanus rodgersii*. Data are relative yields of advanced 2-arm plutei generated at each temperature treatment expressed as a percentage of the total number of advanced 2-arm plutei produced per trial (means ± SE of n=3 trials). Accompanying image is of a 2-arm pluteus larva at 21 days post fertilisation (scale bar = 200μm).

short 1 month spawning period; mid-NSW populations spawned over several months; while southern populations spawned over 5-6 months (Byrne et al. 1998). *C. rodgersii* may undergo prolonged low intensity 'dribble' spawning over a longer period in eastern Tasmania (a more detailed histological examination of gonads is required), however, it is clear that the main period of gamete release, indicated by abrupt changes in the GI, occur over a 1–2 month period.

The magnitude of reproductive investment in eastern Tasmania (max. population GI=20.1 %; max. individual GI=29.3 %) appears to be greater than that within the native NSW range where relatively low GIs (max. population GI≈14 %) have been reported (King et al. 1994; Byrne et al. 1998). This pattern is diametrically opposite that of many other studies, chiefly of terrestrial plants, which describe trends of decreasing reproductive output toward the edges of species' ranges (e.g. Woodward 1990; Despland & Houle 1997; García et al. 2000; Jump & Woodward 2003). The high population GIs at the southern range limit of *C. rodgersii* likely reflects abundant food provided by dense Tasmanian macroalgal beds in combination with lower population densities compared to the dense populations and widespread barrens with limited food on the NSW coast (Byrne et al. 1998; Blount & Worthington 2002; Worthington & Blount 2003). The notion that Tasmanian populations, within macroalgal habitat, are not food limited is further supported by the large individual size attained by *C. rodgersii* in eastern Tasmania. Individuals were commonly observed above the 120 mm maximum test diameter (TD) reported in NSW (Andrew & Byrne 2001), with the largest individual recorded at 133 mm TD and weighing ~ 600 g (drained of coelomic fluid). Furthermore, the GI cycle in eastern Tasmania tracked the temporal cycle in gut index indicating a normal pattern of echinoid food acquirement and subsequent transfer of energy reserves to gonad production (*see* Byrne et al. 1998 for histological examination), emphasising the importance of food availability in procuring large GIs.

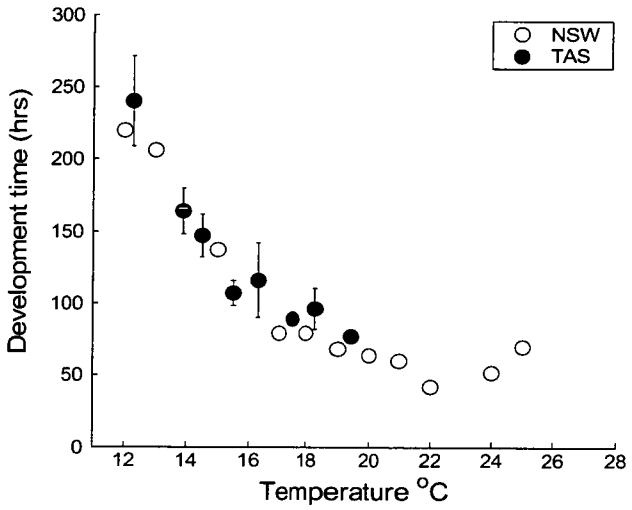

Figure 6. Development time to early 2-arm plutei versus water temperature for Tasmanian and NSW reared *Centrostephanus rodgersii*. Data for Tasmania are means derived from 3 trials (±SE); for NSW, data is means from King 1992 (SE not available). Note: data from the 20.3 °C temperature for Tasmania has been omitted from this plot due to evidence of heat stress in this treatment.

Lack of adaptive shift in temperature dependency of larval development

The strong reproductive condition of Tasmanian *C. rodgersii* was reflected in viable gamete production and larval development in accordance with normal patterns described for *C. rodgersii* from NSW (King 1992; King et al. 1994; Huggett et al. 2005; *see* Figure 4). While there was little detectable effect of temperature on fertilisation success at temperatures ranging from 8 to 20 °C, there was a strong effect of water temperature on larval development. Larval development was poor below 12 °C, and optimum larval yields and developmental rates occurred at ~14-16 °C. Importantly, Tasmanian *C. rodgersii* larvae appear to develop at similar rates to their counterparts in warmer NSW waters (Figure 6). The only evidence for deviation in rates of development was the poor performance of Tasmanian reared larvae at the warmest temperature examined (20.3 °C). This may indicate heat stress to gametes and/or embryos at temperatures ≥8 °C higher than the ambient temperatures experienced by parents. Moreover, there was no evidence of acclimation of larvae to cooler Tasmanian waters since a similar larval development threshold of ~12 °C is also evident in NSW (King 1992). This finding supports the 'recent' nature of the *C. rodgersii* range extension given that adaptive shifts to thermal tolerance would likely require many generations to evolve within the cooler Tasmanian environment.

Lack of adaptive shift in reproductive phenology

The observation that Tasmanian *C. rodgersii* undertook spawning in water temperature below 12 °C in 2004 (Figure 2d) is intriguing given that gametes would have been released into a temperature environment unsuitable for successful larval development (Figures 4&5). Such a counter-productive strategy strongly suggests that *C. rodgersii*

reproductive phenology has not undergone adaptive shift and is controlled by factors other than temperature. This contention is supported by research within the NSW range where consistencies in the timing of spawning of *C. rodgersii* occurred across 9 degrees in latitude even though large temperature gradients were present over this range (Byrne et al. 1998). Photoperiod coinciding with the winter solstice appears as a likely proximate factor cuing the onset of spawning across this broad geographic range (Byrne et al. 1998 and references therein), as has been found in other closely related echinoid species (Kennedy & Pearse 1975; Coppard & Campbell 2005).

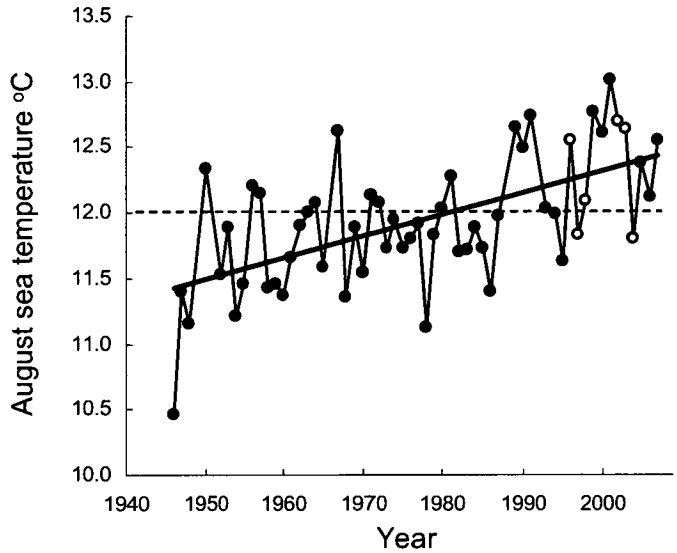

Figure 7. Long-term winter warming trend of coastal waters in eastern Tasmania, 1946-2007. Data are sea temperatures from the Maria Island coastal station (148° 13' E, 42° 36' S) averaged across depth (0-50 m) for August, i.e. the month of major spawning (data courtesy of CSIRO Marine & Atmospheric Research). Note that the water column is mixed across this depth range during August. Dashed horizontal line indicates the 12 °C larval development threshold for Tasmanian *C. rodgersii*. Open symbols represent robust satellite derived estimates of sea surface temperature at the long-term station for recent years with missing *in situ* data (*see* Ridgway 2007).

Mismatches between reproductive rhythms entrained by photoperiod and suitable temperatures for early development are predicted to become commonplace as accelerating climate change impacts on phenologies and ultimately the ranges of many species (e.g. Parmesan & Yohe 2003). For species dispersed poleward by changing climate patterns, delay in establishment of reproductively viable populations is likely unless local climate is dually warmed above physiological thresholds or adaptive shifts in phenology and/or physiology is immediate. From an increasing number of examples of species undergoing adaptive shifts to climate change, these shifts are not immediate but require evolutionary time scales, and shifts in phenology are anticipated to precede shifts in thermal optima or increased thermal tolerance (Bradshaw & Holzapfel 2006).

Future trends in reproduction

Given that Tasmanian reared *C. rodgersii* displayed normal embryonic and larval development to the 2-arm pluteus stage within 12–20 °C (Figure 4), it is likely that the sea urchin successfully propagates larvae throughout its current Tasmanian range in years when the winter temperature during the major spawning period is ≥~12 °C. Hart and Scheibling (1988) report evidence of an analogous temperature threshold mechanism for *Strongylocentrotus droebachiensis* along the Atlantic coast of Nova Scotia where sea urchin population booms and associated overgrazing of kelp beds were correlated with a positive ocean temperature anomaly allowing optimal temperatures for larval development. Long-term monitoring of sea surface temperature in eastern Tasmania has revealed a ~1.5 °C warming over the past 60 years, predominantly due to a greater influence of the East Australian Current on this coast (Ridgway 2007). Importantly, this warming trend is also apparent during winter months, such that temperatures above the ~12 °C threshold for larval development are becoming frequent during the major spawning period (Figure 7) and are likely to arise with increasing frequency given anticipated ongoing coastal warming associated with global climate change (Cai et al. 2005). Continued coastal warming will also reduce larval development time (Figures 4 & 6) which may in turn enhance larval survival and increase the likelihood of self-recruitment of *C. rodgersii* within Tasmania due to decreased exposure to potentially hazardous planktonic conditions (e.g. Morgan 1995). Thus the long-term winter warming of eastern Tasmanian coastal waters and projected trend(s) under global climate change is leading to an environment more conducive for *C. rodgersii* development. Finally, by combining a trend of increasing population size with reproductive capability, this suggests that aided by a new thermal regime, *C. rodgersii* has established viable populations along the eastern Tasmanian coastline.

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CHAPTER 3: CLIMATE DRIVEN RANGE EXTENSION OF A SEA URCHIN: INFERRING FUTURE TRENDS BY ANALYSIS OF RECENT POPULATION DYNAMICS

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Abstract

Patterns of climate forced range-shift in the marine environment are informed by investigating population dynamics of an ecologically important sea urchin (*Centrostephanus rodgersii* - Diadematidae) across its newly extended range in Tasmania (SE Australia). A growth model of *C. rodgersii* is developed allowing estimation of a sea urchin age profile and, in combination with abundance data, we correlate the sea urchin population dynamic with respect to environmental signals across the range-extension region. Growth patterns did not vary across the extension region however there was a strong pattern of decreasing sea urchin age with increasing distance from the historic range. The sequential poleward discovery of the sea urchin, a pattern of declining age and a general poleward reduction in abundance along the eastern Tasmanian coastline is consistent with a model of range-extension driven by recent change to patterns of larval dispersal. We explore this hypothesis by correlating *C. rodgersii* population characteristics with respect to the East Australian Current (EAC), i.e. the chief vector for poleward larval dispersal, and reveal patterns of declining sea urchin age and abundance with increasing distance from this oceanic feature. Furthermore, *C. rodgersii* is generally limited to sites where average winter temperatures are warmer than the cold threshold for its larval development. Potential dispersal and physiological mechanisms defining the range-extension appear strongly coupled to EAC dynamics which has undergone recent poleward advance and resulted in coastal warming in eastern Tasmania. Predicted climate change conditions for this region will favour continued population expansion of *C. rodgersii* not only via atmospheric forced ocean warming, but also via ongoing intensification of the EAC driving continued poleward supply of larvae and heat.

Introduction

Given the range of climate change projections (*reviewed by* Meehl et al. 2007), impacts on the distribution of marine species are likely to be profound. Anticipating responses of marine biota to climate change necessitates an understanding of how changed physical patterns will modify processes currently defining the distribution of marine populations. While species distributions are widely anticipated to shift poleward as a result of latitudinal shifts in bio-climate envelopes (e.g. Pearson & Dawson 2003; Hijmans & Graham 2006), the applicability of such models has been rarely assessed for marine environments (*but see* Lima et al. 2007). Given that re-distribution of marine species is already occurring in response to recent climate change, generalized predictive models of marine biological responses are likely best informed by examining the physical and physiological context of marine populations already shifting (e.g. Barry et al. 1995; Holbrook et al. 1997; McGowan et al. 1998; Sagarin 1999; Zacherl et al. 2003).

In the southern hemisphere, the south eastern coast of Australia has been identified as a climate change hotspot (Poloczanska et al. 2007; Ridgway 2007a). Here the East Australian Current (EAC) has strengthened resulting in greater poleward penetration of warm water over the past 60 years and an approximate doubling of ocean warming rates compared to the global ocean average (Ridgway 2007a). This pronounced change in the physical oceanography of the region corroborates with a series of recent poleward range extensions (*reviewed by* Poloczanska et al. 2007); with changes in both advective patterns and increased water temperature suggested as direct drivers of range extension in the worlds oceans (e.g. Fields et al. 1993; Gaylord & Gaines 2000; Harley et al. 2006). The physical and biological expression of changes in the dynamics of the EAC is clearly evident on the east coast of Tasmania where oceanographic data reveal rising water temperature and salinity due to this feature (Ridgway 2007a) and where species typical of warmer northern waters now occur (e.g. Edgar 1999, 2000; *reviewed by* Poloczanska et al. 2007).

Of those species recently established in Tasmania, the diadematid sea urchin *Centrostephanus rodgersii* (Agassiz) is arguably the most conspicuous and ecologically important due to its ability to catastrophically overgraze seaweed beds and maintain an alternative and stable barrens habitat (Andrew & Byrne 2001; Hill et al. 2003; Ling 2008). Indeed, such is the impact of *C. rodgersii* on reef biodiversity that, within the extended Tasmanian range, overgrazing by this species results in localised losses of ~150 taxa that associate with seaweed beds (Ling 2008). In south-eastern Australia, *C. rodgersii* has historically been restricted to the coast of New South Wales (NSW, see Figure 1), and while adult *C. rodgersii* remain highly localised on rocky reefs (*reviewed by* Andrew & Byrne 2001), the sea urchin possesses a long-lived pelagic larval stage of ~100 days (Huggett 2005) that has considerable potential for long-distance dispersal via ocean currents. Thus, it has been suggested that the poleward range extension of *C. rodgersii* to Tasmania may have occurred due to increased larval dispersal (Edgar 1999; *reviewed by* Andrew & Byrne 2001; Johnson et al. 2005) driven by the poleward advance of the EAC by ~350 km over the past 60 years (Ridgway 2007a). Furthermore, *C. rodgersii* is now reproductively viable in eastern Tasmania as coastal warming has led to a temperature regime warmer than the

12 °C cold limit for successful larval development in this species (Ling et al. 2008). Thus, the potential for population increase and widespread grazing impacts by *C. rodgersii* may be considerable and thus poses a major threat to rocky reef biodiversity (Ling 2008) and associated fisheries in Tasmania (worth ~AUS$150 M pa beach price) that depend on seaweed bed habitat (Johnson et al. 2005).

Given the recent range-extension of *C. rodgersii*, the aim of our study was to document the recent population dynamics of the sea urchin across the range-extension region and search for patterns that may inform future trends of this ecologically important species. Specifically, we develop a sea urchin growth model to determine the age dynamic across the extension-region; then, in combination with patterns in sea urchin abundance, we use a correlative approach to examine the hypothesis that the population dynamics of the sea urchin reflects the new oceanographic regime of the extension-region.

Methods

Population structure of *Centrostephanus* across the newly extended range

Growth and age patterns

A model of *Centrostephanus rodgersii* growth was derived from annual growth increments of tagged individuals living in seaweed dominated habitat on rocky reefs in north eastern (St. Helens) and south eastern Tasmania (Tasman Peninsula) (Figure 1). Individuals were tagged with tetracycline and growth increment data obtained from the change in length of jaw structures (demipyramids) (*after* Ebert 2004; Pederson & Johnson 2008). Jaws were used because they readily stain with fluorescent tetracycline and are widely accepted as the best structure to obtain highly precise measurement of sea urchin growth (Ebert 2004; Pederson & Johnson 2008). Annual growth in jaw length (JL) was obtained for *C. rodgersii* ranging from 61 – 133 mm test diameter (TD) (note that the relationship between JL and TD for Tasmanian *C. rodgersii* was described by the linear allometric equation TD = 4.12 x JL, R^2=0.81, n= 1484). During July-September 2004, approximately 300 *C. rodgersii* were obtained from each tagging site (*see* Table 1) by divers systematically collecting sea urchins from permanently marked plots (~8 m by 8 m) located within seaweed dominated reef habitat. Sea urchins were measured for TD with knife-edge vernier callipers, tagged by injecting 2–4 ml (depending on size) of tetracycline-HCL (conc. 20 gL^{-1} seawater) through the peristomial membrane, and then returned to the marked plots. Tagged urchins were allowed to grow for at least 12 months *in situ* before recapture was attempted. As marked animals could not be identified in the field, recovery of tagged animals involved collecting all sea urchins from within the marked plots and to a distance of 5 m around the plots (Table 1). For each sea urchin collected, TD was measured and the Aristotles' lantern removed and placed in 12.5 % sodium hypochlorite for 48 hrs to expose individual jaw structures. Jaws were then checked under UV light for the presence of a fluorescing tetracycline mark and, if present, the jaw growth increment (ΔL) was measured to nearest 0.05 mm (*after* Pederson & Johnson 2008).

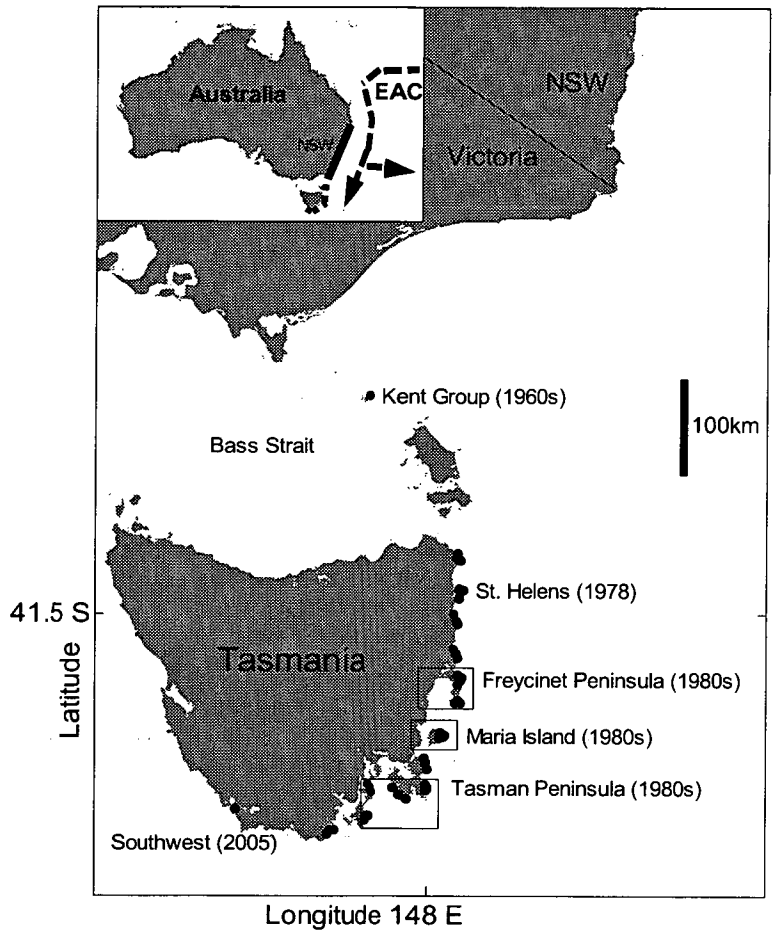

Figure 1. Map of south eastern Australia showing sites where *Centrostephanus rodgersii* age structure (filled circles) and density (open circles, data from Johnson et al. 2005) were determined in Tasmania. The timing of first sightings of *C. rodgersii* along the Tasmanian coastline is shown in parentheses (*after* Johnson et al. 2005). Inset displays mainland Australia and the direction of the East Australian Current (EAC); the 'native' distribution of *C. rodgersii* (solid line, *after* Andrew & Byrne 2001); and the recent range expansion of the sea urchin (broken line). Boxes on eastern Tasmanian mainland indicate 3 locations where temperature was compared between headland (offshore) and inshore sites.

Selection and fitting of growth model

For tag-recaptured *C. rodgersii* in eastern Tasmania, the pattern of annual ΔL versus initial jaw size at tagging (L_t) indicated an indeterminate growth pattern which was well described by an inverse logistic function (*see* Rodgers-Bennett et al. 2003; Haddon et al. 2008). Optimum fits for the inverse logistic functions were determined by minimising the sum of the negative log-likelihoods for each of the observed jaw growth increments (ΔL) and the expected jaw growth increments derived by the model. The expected variation around the growth increments was explicitly modelled as a

power function of the expected length (*after* Haddon et al. 2008). The Inverse Logistic equation is written as:

$$\Delta L = \frac{Max\Delta L \times \Delta_t}{1 + e^{Ln(19)\frac{(L_t - L_{50}^m)}{(L_{95}^m - L_{50}^m)}}} + \varepsilon_{L_t} \qquad \text{eqn. (1)}$$

Where, $Max\Delta L$ is the hypothetical asymptotic maximum jaw growth increment at some initial jaw size that sets the exponential term to zero, Δ_t is the actual time increment between tagging and recovery, i.e. one year. L_t is the jaw length when first tagged, L^m_{50} is the initial jaw length at which the mid-way point between the $Max\Delta L$ and zero growth increment is reached, L^m_{95} denotes the initial jaw length at which 95% of the difference between zero and maximum increment is reached. The error term εL_t is additive and normal, and assumed to have a mean of zero and standard deviation σ_{Lt}, which is also defined as a function of predicted length (*see* Haddon et al. 2008).

Table 1. Summary of tetracycline tagging of *Centrostephanus rodgersii* in north east (St. Helens) and south-east (Tasman Peninsula) Tasmania. Growth models were generated from growth increment data standardised to 365 days growth. Size range of tagged urchins recovered was 61 – 133 mm TD (or 13.8 – 31 mm jaw length).

Site	No. tagged	Date of Tagging	Date of Recovery	Days at liberty	No. urchins collected	No. tagged urchins recovered
St. Helens						
Site 1	341	28/07/2004	22/09/2005	421	731	153
Site 2	383	17/08/2004	11/10/2005	420	660	89
Tasman Peninsula	250	12/09/2004	7/10/2005	390	289	189
Total	974				1680	431

Estimating age distributions from size distributions

Size-frequency distributions of *C. rodgersii* were obtained by measuring jaw lengths (and TDs) for a total of 1706 urchins from 6 locations spanning the Tasmanian range (Figure 1). Age-distributions for each location were then constructed by determining age-at-given size for each individual from the logistic growth model. Given variability in the generalised growth model, there was relatively low confidence in the absolute nature (accuracy) of the predicted ages, e.g. from the model, an individual of 75 mm TD could be 6-10 years old; and a 100 mm TD individual could be 12–22 years old. Importantly however, because growth patterns were consistent in NE and SE Tasmania (growth trajectories between sites were compared using likelihood ratio tests, *after* Haddon 2001), the generation of age frequencies with this method provided an unbiased and precise tool for broad scale examination of *C. rodgersii* age structure in eastern Tasmania. To allow for slight differences in collection times between sites, age was standardised to the 22 December 2005.

Spatial distribution of Centrostephanus across the newly extended range

The spatial distribution of *C. rodgersii* on the east coast of Tasmania was obtained from dive surveys conducted during 2001-2002 (Johnson et al. 2005). This survey involved a spatially hierarchical sampling design based on 13 eastern Tasmanian locations with 3 sites per location (Figure 1). The density of *C. rodgersii* at each site was estimated from 4 replicate belt transects, each 2 m wide and extending from ~6 m to the bottom edge of the reef or to a maximum depth of 18 m (*for details see* Johnson et al. 2005). Data on *C. rodgersii* density additional to the primary survey was obtained for the Kent Group of Islands (2005), and south-west Tasmania (2005-2006), giving a total of 41 sites. For the 6 locations where age structure was estimable, the abundance of *C. rodgersii* was modelled as a function of average urchin age.

Patterns in the environment across the newly extended range

Proximity to source populations

For the *C. rodgersii* population to have spread sequentially poleward from the historic NSW range across eastern Tasmania, then within the extension region there should be a pattern of younger ages and lower population density with increasing distance from the native range of the sea urchin. Alternatively, if the population has arisen and spread following a rare recruitment/ anthropogenic translocation event to a particular Tasmanian site, then the expectation would be for a punctuated distribution of abundance and ages within the vicinity of a founding population. To examine patterns in age and abundance of *C. rodgersii* across the newly extended range, the edge of the native range was assigned to be the NSW-Victorian border (Figure 1).

Because the EAC is the major current system in south eastern Australia and the chief mechanism enabling poleward transport of water mass and larvae from NSW to eastern Tasmania, we hypothesised that *C. rodgersii* populations should, on average, be more abundant and of older average age with closer proximity to this current system (based on the likelihood of cross-shore diffusion of larvae, e.g. Largier 2003). Alternatively, if *C. rodgersii* populations in eastern Tasmania are not associated with this environmental signal then it would suggest that other abiotic or biotic factors are more important in driving the observed range extension. Proximity to the EAC was determined by estimating the position of its western margin based on the distribution of isotherms generated from averaged SST maps over the period 1992-2006 (SST Pathfinder, 4 x 4 km interpolated pixels). Note that while the EAC extension is widely recognized as a predominantly summer phenomenon in south eastern Australia (Ridgway 2007a&b), the western margin of this oceanographic feature from the NSW-Victorian border south was most strongly demarcated as the 12.9 °C isotherm during winter when atmospheric cooling of neighbouring water masses clearly revealed the proximal edge of this warm feature. Average age at each of the 6 locations where age was estimable was therefore regressed against proximity to NSW-Victorian border and proximity to the western edge of the EAC. Abundance of *C. rodgersii* was also regressed against distance to the NSW-Victorian border (native range) and proximity to the EAC.

Winter climate across the newly extended range

Species undergoing poleward range-extension will be most physiologically challenged during cold winter conditions. Given that the cold water threshold for *C. rodgersii* larval development is 12 °C and that coastal water temperatures in eastern Tasmania during the winter spawning period (August) fluctuate about the 12 °C threshold (Ling et al. 2008), we examined the distribution of *C. rodgersii* abundance with respect to winter climate across Tasmania. We hypothesized that the abundance of *C. rodgersii* in eastern Tasmania should reflect this lower physiological limit of the sensitive larval phase, i.e. sites where winters are warmer should be more suitable habitat for *C. rodgersii* larvae to develop and settle, thus adult populations should be larger. Using the population density of *C. rodgersii* as a proxy for recruitment, we correlated density of *C. rodgersii* with respect to the average August (coldest winter month) temperature obtained from remotely sensed SST imagery available for 1992-2006 (SST Pathfinder). Note that the average August SST for each site was interpolated from the surrounding 4 x 4 km pixel and to avoid distortion from coastal landmasses sites were offset seaward by 4 km. Furthermore, because the sea surface temperature was obscured on days of cloud cover, each daily temperature estimate was calculated as the running mean for ±3 days about the day of interest.

Local-scale patterns: Headlands versus embayments

Observations of the distribution of *C. rodgersii* in eastern Tasmania suggest an association of the sea urchin with headlands along this coastline (S. Ling *pers. obs.*; *also see* Johnson et al. 2005). This pattern contrasts with that observed within the native range of *C. rodgersii* where the sea urchin is found abundantly throughout headlands and embayments (Andrew & Byrne 2001). We therefore compared inter-annual SST signals for rocky reef habitats at headlands and adjacent inshore reefs at three locations where SST data and estimates of *C. rodgersii* density were available (*see* Figure 1). The density of *C. rodgersii* was then examined with respect to the proportion of winters in which the temperature regime existed above the 12 °C cold threshold for *C. rodgersii* larval development. Additional sea temperature data were obtained at headlands and embayments from calibrated *in situ* loggers (N=7, Optic Stowaway WTA08-05+37 by Onset®, accuracy ± 0.2 °C) fixed to reef at a depth of 9 m.

Results

Population structure of *Centrostephanus* across the newly extended range

Growth patterns of *C. rodgersii* across sites in eastern Tasmania were highly similar (likelihood ratio test between St Helens and Fortescue sites indicated no difference, P=0.45, with almost total overlap of the 99% bounds around the residuals). Thus, all growth increment data were pooled to derive a generalised growth model for *C. rodgersii* in eastern Tasmania. Annual growth of *C. rodgersii* jaws was best described by an inverse logistic model (indeterminate growth) (Figure 2a). From this model, age at a given jaw length (Figure 2b) and age at a given test diameter (Figure 2c) were estimated. Estimation of age structure from size distributions for 6 locations spanning the Tasmanian range of *C. rodgersii* revealed a pattern of younger ages with increasing

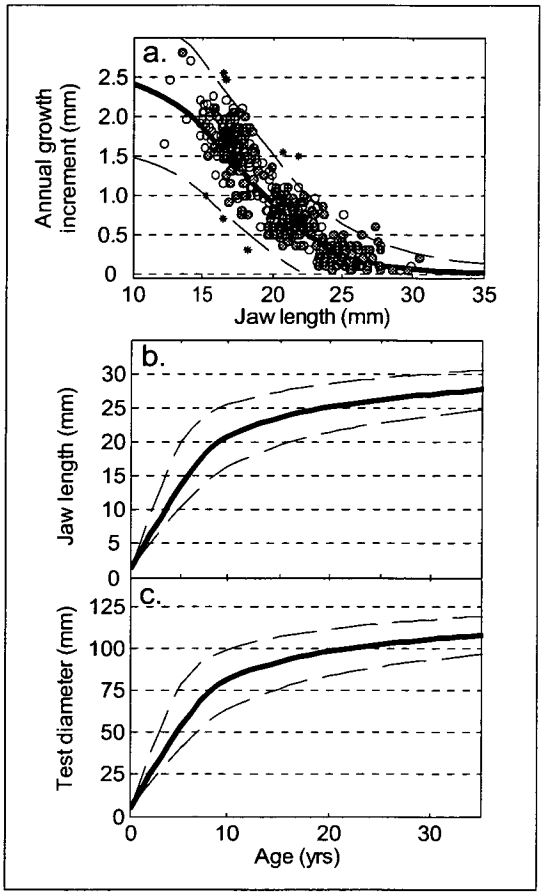

Figure 2. Growth of *Centrostephanus rodgersii* in macroalgal habitat in eastern Tasmania. (a) Generalised *C. rodgersii* growth model in macroalgal habitat in eastern Tasmania based on annual jaw growth. Closed circles are data for St. Helens, open circles are for Fortescue Bay. The seven samples represented as stars in panel (a) were removed from the analysis being identified as outliers from the spread of residuals. The optimal inverse logistic parameters for eqn (1) were $MaxΔL$=2.599 mm, L^m_{50}=17.994 mm, L^m_{95}=27.290 mm. From this equation jaw length at age is predicted (b), and test diameter at age (c). Test diameter is determined from the allometric relationship between test diameter (TD) and jaw length: TD = 4.12 x (Jaw Length), R^2=0.81. In all panels solid lines represent the median model fit generated from 1000 bootstrap simulations and broken lines indicate 95% confidence intervals.

poleward (southward) extent. Northern locations contained populations represented by a broad range of predicted ages including many older individuals. Moving southward, age distribution became dominated by younger individuals with relatively few old individuals represented (Figure 3). Across the extension-region, the density of *C. rodgersii* was positively related to mean population age (y =0.031x + 0.2, R^2 =0.70).

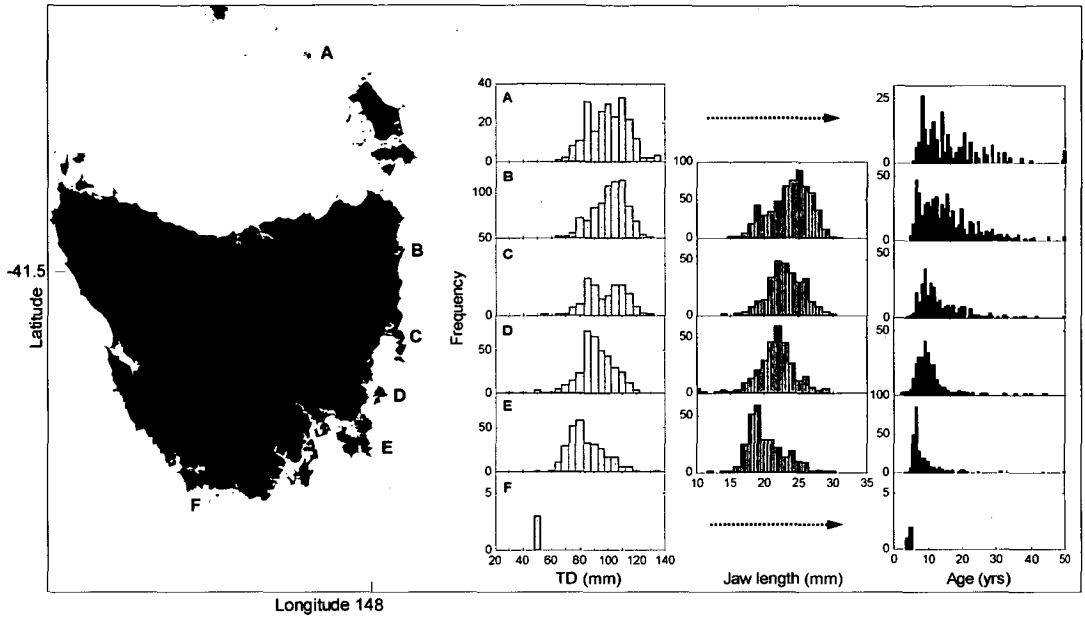

Figure 3. Spatial pattern of *Centrostephanus rodgersii* size and age structures in eastern Tasmania. A=Kent Group, *n*=222; B=St. Helens, *n*=600; C=Freycinet Peninsula, *n*=300; D=Maria Island, *n*=300; E=Tasman Peninsula, *n*=281; F=South west Tasmania, *n*=3. Note that age frequencies for Kent Group and south-west Tasmania were generated by converting test diameters to jaw lengths using the generalised allometric relationship for eastern Tasmania.

Correlative patterns across the newly extended range

Mean SST patterns reveal the dominant influence of the EAC on coastal waters in south east Australia, including eastern Tasmania (Figure 4a). Across the range-extension region of *C. rodgersii*, mean population age of the sea urchin was negatively related to increasing distance from the southern limit of the sea urchins historical range (i.e. the NSW/ Victorian border) (Figure 4b); and evidence for an exponential decline in mean age was observed with increasing distance from the western edge of the EAC across eastern Tasmania, but not for Bass Strait where the Kent Group appeared anomalous to this pattern (Figure 4c). The local abundance of *C. rodgersii* across the extension-region (i.e. no. of sea urchins m^{-2} of rocky reef) versus proximity to population sources also revealed evidence of negative, but noisy, correlations with distance from the historical range(Figure 4d) and distance from the western edge of the EAC (Figure 4e). Note that proximity of the historical range of *C. rodgersii* did not simply co-vary with proximity to the western edge of the EAC; for eastern Tasmania (NE to Tasman Peninsula, but excluding the anomalous Kent Group) a slight negative correlation was observed (linear fit, $EAC_{prox.} = -0.037 * historic_{prox.} + 43.75$, $R^2 = 0.46$,); meanwhile, a strong positive relationship was described for sites in southern Tasmania where *C. rodgersii* was rare (linear fit, $EAC_{prox.} = 0.62\ historic_{prox.} - 356.48$, $R^2 = 0.42$).

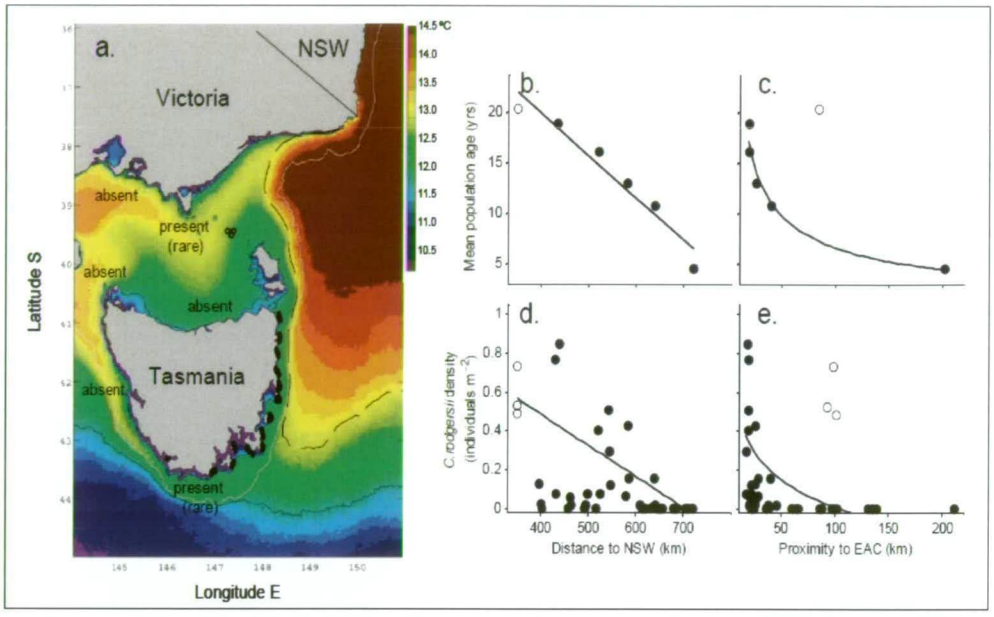

Figure 4. (a) SST map showing influence of the EAC in eastern Tasmania (data are means for August 1993-2007); western edge of the EAC is shown as broken line; also shown is presence/ absence of *Centrostephanus rodgersii* for locations west of NSW/ eastern Tasmania. (b) Regression of mean population age of *C. rodgersii* against proximity to native range, y=-0.042x + 36.66, R^2=0.94, filled symbols are for mainland Tasmania, open symbols are for the Kent Group. (c) Mean population age versus distance to the mean position of the western margin of the EAC 1992-2006; data across mainland Tasmania (excluding Kent Group) displays a negative exponential, y=87.46$x^{-0.56}$, R^2=0.98. (d) Density of *C. rodgersii* in eastern Tasmania versus distance to native range; linear trendline represents 'ceiling' of the distribution obtained by regression of highest ranking sites within each location, y=-0.0016x+1.1276, R^2=0.41. (e) Density of *C. rodgersii* in eastern Tasmania versus proximity to the EAC; log trendline represents 'ceiling', as per (c), but excluding Kent Group, y=-0.2036Ln(x) + 0.95, R^2 = 0.41.

Examination of mean SST for 41 eastern Tasmanian sites during the known *C. rodgersii* spawning period of August (winter), revealed that the sea urchin is generally limited to sites experiencing relatively warm winter temperatures in eastern Tasmania (Figure 5a). Inter-annual SST profiles across eastern Tasmania (for the period 1993-2006) revealed a clear pattern of increasing local abundance of *C. rodgersii* with an increasing proportion of winters experiencing temperatures warmer than the 12 °C cold water threshold for larval development (Figure 5b). Examination of sea temperature profiles on headlands, where *C. rodgersii* was abundant, also revealed warmer winter temperatures at these sites and a greater proportion of winters >12 °C, relative to adjacent inshore sites where fewer or no *C. rodgersii* were established (Figure 6a-c).

Discussion

Poleward decrease in age

Within the recently extended range of *Centrostephanus rodgersii*, mean population age became progressively younger towards the poleward range limit. This age dynamic is therefore consistent with the historical time-course of sequential poleward discoveries and expansion of *C. rodgersii* populations across eastern Tasmania, which has occurred at a rate of ~160 km decade^{-1} over the past 40 years (Johnson et al. 2005, *see* Figure 1). Furthermore, the broad range of *C. rodgersii* ages in north eastern Tasmania indicates that the range extension has not occurred as the result of a single, massive recruitment event. Rather, there appears to have been multiple episodes of sea urchin recruitment with seemingly fewer and more recent recruitment events towards the southern limit of the extension-region. Indeed, analyses of genetic diversity of *C. rodgersii* from the within the extension-region and historical regions of the species' range yield no evidence of a founder effect, suggesting continued supply of individuals from within the historical range (Johnson et al. 2005; Banks et al. 2007). Given that the benthic phase of *C. rodgersii* is reef bound and lack of contiguous reef habitat from the historic range to the range extension region (i.e. across Bass Strait, *see* Figure 1), migration of the sea urchin to Tasmanian waters must have occurred, and most likely continually occurs via a highly dispersive pelagic larval phase. The only alternative would be continual migration via direct anthropogenic translocation of adult individuals via vectors such as shipping, however, patterns in population spread, age structure, genetic signals (*op cit*) and port locations provide no evidence supporting the existence of such a mechanism.

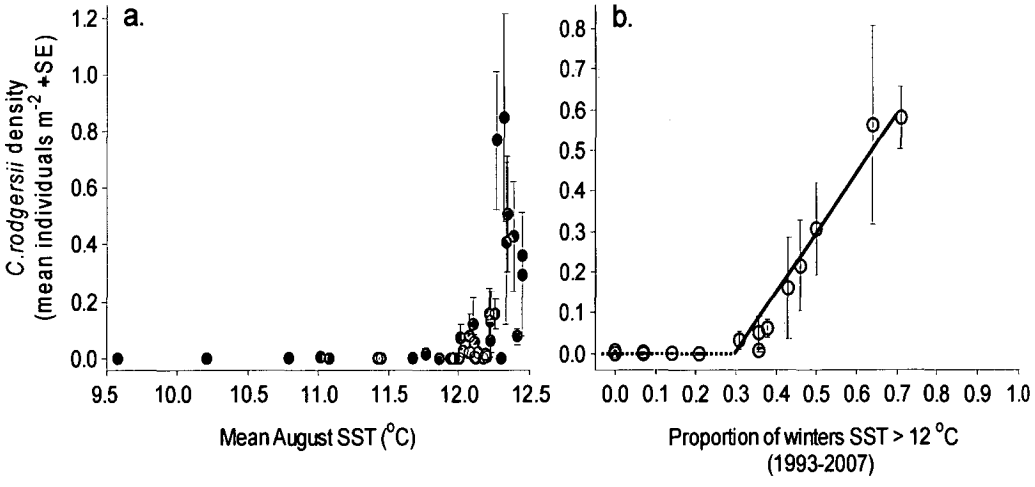

Figure 5. (a). Abundance of *Centrostephanus rodgersii* as a function of mean August temperature (mean SST derived from satellite images for the period 1993-2006) for 41 sites in eastern Tasmania. (b). Abundance of *Centrostephanus rodgersii* as a function of proportion of winters (July-Aug-Sep, 1993-2006) where mean temperature was greater than the 12 °C larval development threshold (after Ling et al. 2008); linear trendline fitted to data where x values > 0.3, $y = 1.4044x - 0.4143$, $R^2=0.93$.

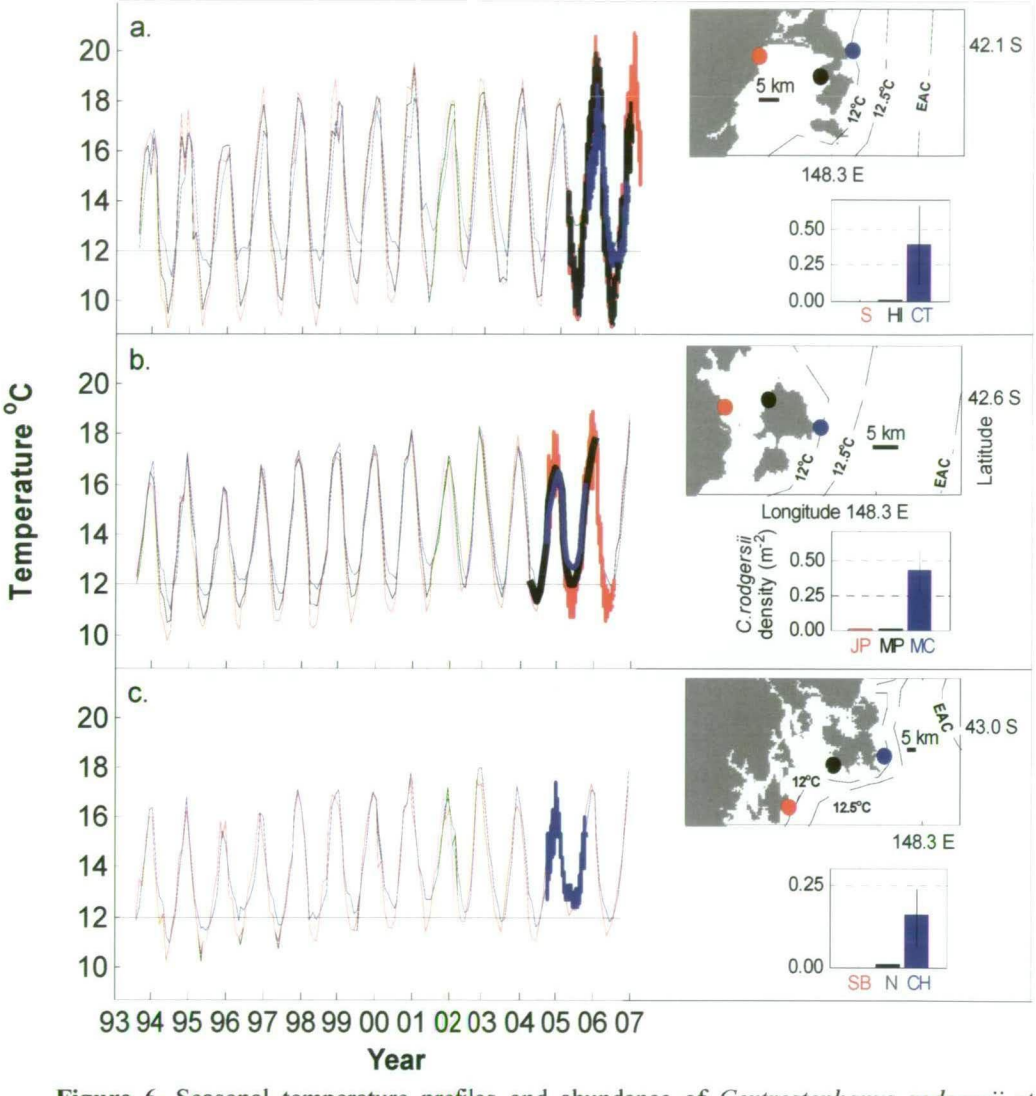

Figure 6. Seasonal temperature profiles and abundance of *Centrostephanus rodgersii* at 'headland' and adjacent inshore reefs. Data are SST for 1993-2007; thickened lines are data obtained from *in situ* temperature loggers. Horizontal bar on temperature plots indicates the lower temperature threshold (12 °C) for *C. rodgersii* larval development (*after* Ling et al. 2008); numbers in parentheses indicate proportion of winters > 12 °C at each site for 1993-2007. (a). Freycinet Peninsula: CT=Cape Tourville (0.43); HI=Hazards Is. (0.00), S=Swansea (0.00); (b). Maria Island: MC=Mistaken Cape (0.46), MP=Magistrates Pt. (0.00), JP=Johnson's Pt. (0.00); (c). Tasman Peninsula: CH=Cape Huay (0.38), N=Nubeena (0.07), SB=South Bruny (0.07). For locations within Tasmania, refer to Figure 1. On maps, isotherms and western EAC margin represent mean positions for winter 1993-2006. *C. rodgersii* abundance data for HI & S, in panel (a), courtesy of N. Barrett.

The positive relationship observed between abundance and age of *C. rodgersii* across the extension-region is consistent with a population undergoing expansion (as documented by Johnson et al. 2005) and suggests a mechanism(s) for continued recruitment of larvae to previously established populations. For *C. rodgersii* to undergo localised population expansion its larvae must either actively seek sites with conspecific adults (e.g. Tegner & Dayton 1977; Rowley 1990), or local coastal hydrodynamics must somehow determine larval supply, or there is differential habitat suitability such that particular sites accumulate cohorts to become abundant and old (e.g. Ebert & Russell 1988; Morgan et al. 2000; Wing et al. 2003). Because of the long-lived planktotrophic larval phase of *C. rodgersii*, dispersal of larvae from parental sites is potentially great. Hence the scale at which larvae could actively seek out adult populations is likely to be small relative to scales over which larvae are potentially dispersed. Therefore, differential exposure of coastal sites to larval supply would appear a plausible mechanism explaining the observed relationship between population abundance and age structure of *C. rodgersii* across the extension-region in eastern Tasmania.

Proximity to larval sources

Supporting a model of range-extension based on larval supply, the proximity of eastern Tasmanian sites to putative population sources of *C. rodgersii* revealed that average age and abundance of the sea urchin not only declined with increasing distance from the southern boundary of NSW (i.e. across a latitudinal gradient), but sea urchin age and abundance were also negatively correlated with distance to the nearshore margin of the EAC in eastern Tasmania. While a decline in abundance with increasing distance (latitude) from a native range may be simply explained by gradual diffusion of the species from a population centre at lower latitude (e.g. Brown's Principle, Brown 1984), in the case of a benthic invertebrate with a highly dispersive larval phase, yet a non-migratory reef-bound adult phase, such a distributional pattern is also likely to reflect opportunity for larval dispersal (e.g. Largier 2003). With respect to the chief mechanism for poleward transport, the EAC, mean age and abundance of *C. rodgersii* were correlated with proximity to this oceanic feature across the range extension region. While this pattern held strongly across eastern Tasmania and while general proximity to the EAC provides a broad biogeographic description of the sea urchins presence throughout the SE Australian region (*see* Figure 4a), the high densities and relatively old ages of *C. rodgersii* within the Kent Group of Islands (eastern Bass Strait) was an exception to this pattern. Intriguingly, the reef biota of the Kent Group, unlike adjacent island groups immediately north (Hogan Group) and south (Flinders Group), is typical of southern NSW (Edgar et al. 1997) and formally classified within the same bioregion (IMCRA 2006). Clearly, some form of connectivity (perhaps relating to the proximity of the warm tongue of 13 °C water observable in north eastern Bass Strait in Figure 4a, or perhaps dynamic inter-seasonal ocean patterns evident in this region, but not captured by our analysis), must be invoked to explain the presence of *C. rodgersii* in the Kent Group and the lack of genetic differentiation between this population and populations in NSW or eastern Tasmania (Johnson et al. 2005).

Winter climate and the cold physiological limit

Because eastern Tasmania represents the southern range extent where coastal waters are cold (~10–18 °C) relative to NSW (~13-25 °C), the observed distribution of *C.*

rodgersii in Tasmania may be due to the moderating influence of the warm EAC along this coast (Ridgway 2007a&b; *see* Figure 4a). Indeed, any limiting effects of cold water on the development and survival of the sea urchin in Tasmania would most likely be felt during winter. Examination of *C. rodgersii* distribution with respect to winter water temperature revealed that the sea urchin is most abundant at sites of relatively warm winter climate (Figures 4a, 5, 6). In eastern Tasmania, warmer sites generally supported higher abundances of *C. rodgersii* relative to nearby colder sites where its abundance was low or the sea urchin was absent altogether (*see* Figure 4a). However, variability in *C. rodgersii* abundance across warmer winter sites suggests that factors other than temperature *per se* are important in determining patterns in abundance such as reef habitat quality (Johnson et al. 2005), or barriers against dispersal of sea urchin larvae (e.g. Gaylord & Gaines 2000). Clearly a model of *C. rodgersii* distribution in SE Australia based purely on a bio-climate envelope of suitable temperature for larval development (i.e. > 12 °C) is inappropriate as the suitable bio-climatic envelope would extend across most of southern Australia. However, *C. rodgersii* is not present on coastlines west of Bass Strait (Figure 4a). Indeed, current mediated dispersal barriers are known to define many biogeographical boundaries in coastal oceans, despite apparently suitable habitat occurring beyond dispersal barriers (e.g. Gaylord & Gaines 2000 *reviewed in* Harley et al. 2006). Similar to our findings, Banks and co-workers (2007) conclude that the oceanographic influence on local genotypic structure of *C. rodgersii* relates to the temporal variability in sea temperature, as opposed to temperature *per se* or other factors that may vary purely across a latitudinal gradient.

The global extent of *C. rodgersii* further suggests that patterns in the EAC are important in determining the biogeography of the species as populations of the sea urchin occurring outside of Australian waters, i.e. in northern New Zealand including the Kermadec Islands (e.g. Schiel et al. 1986) occur where the EAC flows proximal to these sites (Ridgway & Dunn 2003). Demonstrating population connectivity and larval dispersal capability across large scales (>1000s km), *C. rodgersii* populations in NZ also show weak genetic differentiation from SE Australian populations (Banks et al. 2007). Given that variability in SST for the SE Australian region is strongly influenced by southward movement of the EAC (Ridgway 2007; *see* Figure 4a), it is plausible that patterns in local age structure of *C. rodgersii* across the range extension region reflects the supply of larvae driven by patterns of the EAC. Thus variability in the EAC, as a mechanism for dispersal of *C. rodgersii* larvae, appears important in defining large scale (>1000s Km) and local scale (1000s m) distribution of the sea urchin. However, the observed temperature dependency of *C. rodgersii* larvae strongly indicates the potential for a dual role played by the EAC across the range extension-region by providing 1) a physical dispersal mechanism governing larval supply from within the historic range; and 2) poleward transport of heat maintaining localised reef habitats in Tasmania above the thermal threshold for early development. Because *C. rodgersii* populations in eastern Tasmania undergo normal seasonal reproductive activity and can produce viable larvae, it is likely that the sea urchin is capable of self-recruiting and undergoing population expansion within the extension-region when winter temperatures, driven by EAC dynamics, are maintained above the threshold for successful larval development (Ling et al. 2008).

Local scale patterns: Headlands versus embayments

Examination of local scale patchiness in seasonal climate revealed that headland sites, where *C. rodgersii* was abundant, expressed milder winter climates relative to inshore areas where seasonal temperature fluctuated with greater amplitude. Furthermore, headland sites were also closer to the EAC, and they more likely project further beyond potential coastal boundary layers and so may more frequently sample offshore currents (e.g. Shanks 1995; Largier 2003). Thus, the EAC appears to drive milder winter temperature regimes at such headland sites as well as greater larval supply to these sites, whereas the thermal regime of inshore areas appear more influenced by atmospheric forcing as evidenced by higher summer maxima and lower winter minima (Figure 6a-c; *also see* Ridgway 2007a&b).

The pattern of greater apparent recruitment of *C. rodgersii* to headlands across eastern Tasmania contrasts with findings of Ebert and Russell (1988) on the west coast of North America where a negative association between inferred recruitment rates of sea urchins (*Strongylocentrotus franciscanus*) and headlands was reported. In their study, enhanced upwelling of cold water containing fewer urchin larvae was more prevalent at headlands leading to variable recruitment at these sites relative to more uniform coastline and embayments where upwelling was unpredictable and size frequencies indicated a more consistent annual recruitment (*see also* Morgan et al. 2000). In reconciling differences between our study and those of others (i.e. Ebert & Russell 1988; Morgan et al. 2000) it would appear that the presence of headlands *per se* does not determine sea urchin recruitment. Rather it is the interaction of these coastal features with the prevailing oceanic features that appears important in influencing larval dispersal and determining local recruitment patterns for planktotrophic sea urchins (*see also* Banks et al. 2007). Clearly, finer-scale resolution of oceanic influences on *C. rodgersii* distribution and demographics would necessitate the sampling of sea urchin settlement (0+ year class) across multiple sites over several years to determine the nature of putative fine-scale links between sea urchin recruitment and environmental signals.

Latitudinal trends in adult performance?

While the positive relationship observed between *C. rodgersii* abundance and age across the range extension region is consistent with a population undergoing expansion (and corroborates with the observed discovery and expansion of the urchin in Tasmania documented by Johnson and co-workers 2005), alternatively, this pattern may reflect a gradient in adult performance (e.g. Brown's Principle, Brown 1984; Brown et al. 1995). Assuming homogenous recruitment of juveniles across the study locations, natural mortality rates would have to be at least 4 times greater in SE as opposed to NE Tasmania, and up to 25 times greater in southern Tasmania compared to the NE Tasmanian locations, in order to sufficiently account for the observed patterns in age structure (Figure 7a). However, in contrast to poor larval performance, adult *C. rodgersii* in Tasmania are observed to grow to large size at reef sites where sea temperatures readily fall below 12 °C during winter (*see* Figures 5 & 6). While such reefs contain few *C. rodgersii* (*see* Figure 6), sea temperature alone would appear insufficient to drive such large discrepancies in rates of adult mortality given low latitudinal variability in temperature, particularly across exposed coastal sites in eastern

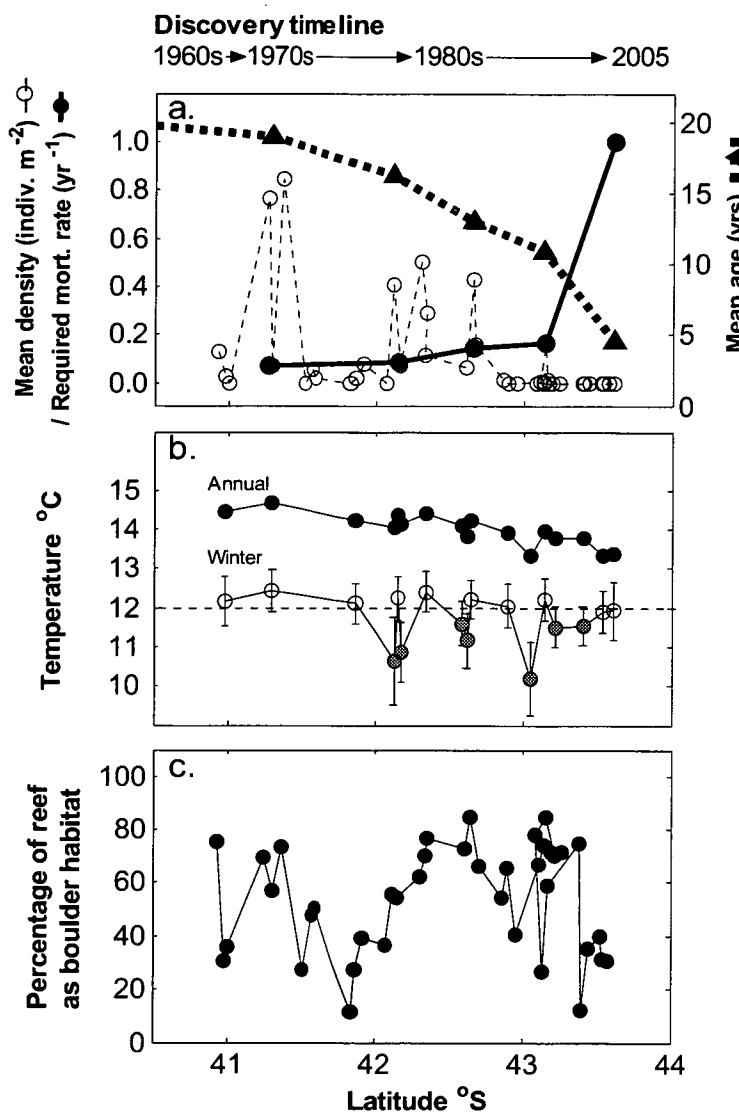

Figure 7. Latitudinal patterns in (a) density of *Centrostephanus rodgersii* (data from Johnson et al. 2005), age, and adult mortality rate (Z estimate) required to generate the observed age-profile across the range-extension region assuming equal larval settlement across locations; (b) mean annual and mean winter sea temperature, note that mean winter temperature consistently exceeds the cold 12 °C physiological threshold for larval development for eastern Tasmanian sites north of Tasman Peninsula 43S); and (c) Availability of preferred boulder habitat for *C. rodgersii* (data from Johnson et al. 2005). For (a), Z was estimated as the negative slope of the natural log of frequencies across age classes (for age classes 7+), *after* Haddon 2001; note that Z refers to natural mortality only as *C. rodgersii* is not currently harvested in Tasmania. Further note, for winter temperatures, i.e. plot (b), filled symbols represent 'embayment' sites, whereas open symbols are exposed coastal locations.

Tasmania (*see* Figure 7a&b). Furthermore, patterns in adult growth rates (Figure 2), dietary composition (S. Ling *unpub. data*) and reproductive output of *C. rodgersii* (Ling et al. 2008) across eastern Tasmania indicate no evidence of declining adult performance with increasing latitude (*also see* Ebert et al. 1999; Byrne et al. 1998; Gilman 2005; Lester et al. 2007).

Another possible explanation is that the pattern of younger ages toward the edge of the extension-region is driven by potential latitudinal trends in mortality rates due to either disease or predation. While disease outbreaks and predators can have major impacts on sea urchin populations (*reviewed by* Steneck et al. 2002); moribund *C. rodgersii* have not been observed in Tasmania (during observations over >8 years, S. Ling *pers. obs.*); and the principal predator capable of consuming *C. rodgersii* in Tasmania, i.e. large spiny lobsters (*Jasus edwardsii*) > 140 mm carapace length (Ling et al. *unpublished manuscript*), have been heavily fished across eastern Tasmania and were rarely observed across all sites from which age frequencies were obtained. Nonetheless, because predation risk is highly size-specific among sea urchins (e.g. Shears & Babcock 2002; Pederson & Johnson et al. 2006; Ling et al. *unpublished manuscript*), younger (i.e. smaller) individuals are more vulnerable to lobster predation, hence expectations for urchin populations experiencing heavy rates of predation would be a bias towards older, not younger, individuals. Furthermore, because *C. rodgersii* prefers boulder habitat where it can seek shelter from predators (Andrew 1993; *reviewed by* Andrew & Byrne 2001), predation risk will be influenced by the availability this preferred habitat type, however the proportion of boulder habitat across the eastern Tasmanian study sites did not reveal a latitudinal gradient (Figure 7c).

Future trends

Typical of benthic marine invertebrates, the chief mechanisms defining the SE Australian range of *C. rodgersii* appear to be dispersal barriers and physiological limits of early life history stages (e.g. Zacherl et al. 2003). That is, a poleward advance of the EAC of ~350 km over the past 60 years (Ridgway 2007a) appears to have dually created opportunity for *C. rodgersii* to undergo range extension by facilitating greater southward transport of larvae and promoting a warming local temperature regime that is now suitable for successful development of the sea urchin within eastern Tasmania. While it was not our goal to explicitly test the contribution of 'temperature' versus 'transport' (e.g. Gaylord & Gaines 2000), the relative importance of each mechanism in defining the range extension/ expansion of *C. rodgersii* in Tasmania may have varied historically and may vary in the future. More importantly, in highlighting links between *C. rodgersii* population trends and the physical environment across the extension-region, our results suggest that ongoing climate change is poised to have further effects on *C. rodgersii* distribution in eastern Tasmania by 1) increasing the extent of thermally suitable reef habitat as a direct result of atmospheric forced ocean warming; and 2) by driving further poleward supply of larvae and accelerating a warmer coastal regime as a result of ongoing intensification of the EAC (as predicted by Cai et al. 2005; Cai 2006). Finally, our results strongly indicate that any generalised prediction of species range-shifts in the marine environment must not only account for shift in bio-climate envelopes, but that the spatial and temporal extent of bio-climate envelops must themselves be defined within the bounds of current driven dispersal potential.

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CHAPTER 4: RANGE EXPANSION OF A HABITAT-MODIFYING SPECIES LEADS TO LOSS OF TAXONOMIC DIVERSITY: A NEW AND IMPOVERISHED REEF STATE

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Abstract

Global climate change is predicted to have major negative impacts on biodiversity, particularly if important habitat-modifying species undergo range shifts. The sea urchin *Centrostephanus rodgersii* (Diadematidae) has recently undergone poleward range expansion to relatively cool, macroalgal dominated rocky reefs of eastern Tasmania (southeast Australia). As in its historic environment, *C. rodgersii* in the extended range is now found in association with a simplified 'barrens' habitat grazed free of macroalgae. The new and important role of this habitat-modifier on reef structure and associated biodiversity was clearly demonstrated by completely removing *C. rodgersii* from incipient barrens patches at an eastern Tasmanian site and monitoring the macroalgal response relative to unmanipulated barrens patches. In barrens patches from which *C. rodgersii* was removed, rapid proliferation of canopy-forming macroalgae (*Ecklonia radiata* and *Phyllospora comosa*) occurred; and within 24 months algal community structure converged with that of adjacent macroalgal beds where *C. rodgersii* grazing was absent. Indeed a notable scarcity of limpets on *C. rodgersii* barrens in eastern Tasmania (relative to the historic range) likely promotes rapid macroalgal recovery upon removal of the sea urchin. In the recovered macroalgal habitat, faunal composition redeveloped similar to that from adjacent intact macroalgal beds in total numbers of taxa, total individuals and Shannon diversity. In contrast, the faunal community of the barrens habitat is overwhelmingly impoverished. Of 296 individual floral/ faunal taxa recorded, only 72 were present within incipient barrens, 253 were present in the recovered patches, and 221 were present within intact macroalgal beds. Grazing activity of *C. rodgersii* results in an estimated minimum net loss of ~150 taxa typically associated with Tasmanian macroalgal beds in this region. Such a disproportionate effect by a single range expanding species demonstrates that climate change may lead to unexpectedly large impacts on marine biodiversity as key habitat-modifying species undergo range modification.

Introduction

Global climate change is predicted to have major negative consequences for marine biodiversity (*reviewed by* Rosenzweig et al. 2007). While impacts on species are widely anticipated to occur directly as a result of shifts in bio-climate envelopes (e.g. Hijmans & Graham 2006), ecosystem effects mediated by range shift of key habitat-modifying species may result in disproportionately large impacts on marine biodiversity (e.g. Hughes 2000; Harley et al. 2006). If habitat-modifying species undergo range shift, the occurrence of 'catastrophic shifts' (Scheffer et al. 2001) in marine ecosystems are likely to become more common with altered ecosystem states having major impacts on biodiversity (e.g. Elmqvist et al. 2003; Folke et al. 2004; Hughes et al. 2005).

Driven by increased poleward penetration of the warm East Australian Current (EAC, *see* Ridgway 2007), the sea urchin *Centrostephanus rodgersii* (Diadematidae) has recently undergone southern range extension in temperate southeastern Australia (Edgar et al. 2004, 2005; Johnson et al. 2005; Ling et al. 2008). Extending its range from New South Wales (NSW) south to the Tasmanian coastline (*see* Figure 1), *C. rodgersii* is just one of many species observed to have undergone recent range extension in this region (Edgar 1997; *reviewed by* Poloczanska et al. 2007). However, it is the range extension of *C. rodgersii* that appears particularly important to the benthic community given the sea urchins' ability to eliminate macroalgal habitat and effect catastrophic shift to an alternative sea urchin 'barrens' state (e.g. Fletcher 1987; Andrew 1991; Andrew 1993; Andrew & Underwood 1993; Hill et al. 2003). Such is the importance of this herbivore that within its historic NSW range approximately 50% of all near-shore rocky reef is urchin barrens as a result of grazing by this single sea urchin species (Andrew & O'Neill 2000).

Since it was first detected off the Tasmanian mainland at St. Helens in 1978, the abundance of *C. rodgersii* has increased, the range has moved further south and widespread barrens habitat (continuous across 100s of metres) now occur in some locations (Johnson et al. 2005). While widespread barrens currently occur in relatively few places in eastern Tasmania, a major feature of *C. rodgersii* grazing on this coast is the occurrence of small incipient barrens patches (1-10s m diameter) within dense and diverse macroalgal beds (Johnson et al. 2005). Given anticipated positive effects of climate change on *C. rodgersii* dispersal and larval development within Tasmania (Ling et al. 2008; *see* Chapters 2&3), barrens habitat could potentially expand on this coastline to reflect patterns already observed in NSW (Johnson et al. 2005). Thus, *C. rodgersii* grazing in eastern Tasmania is considered to pose a major threat to the structure and functioning of the biologically diverse macroalgal-dominated rocky reefs (e.g. Edgar et al. 2004, Ling et al. 2008) and the important resources that they support (Johnson et al. 2005). The aim of this study was to explicitly examine the impact of this range extending species on reef habitat structure and associated biodiversity within the extended range by using controlled sea urchin removals.

Materials and methods

Experimental manipulation

Manipulations testing the effect of *C. rodgersii* grazing on structure and biodiversity of rocky reef within the extended range were undertaken at Bicheno on the east coast of Tasmania (Figure 1). 6 discrete incipient barrens patches ranging in size from ~3–6 m diameter, each supporting 8-116 resident *C. rodgersii* (density 1.3-3.6 m^{-2}), were randomly assigned as complete *C. rodgersii* 'removal' or 'unmanipulated' control patches with no attempt made to standardise urchin numbers across the naturally occurring patches. As described for NSW, *C. rodgersii* in Tasmania is highly nocturnal and displays a homing behavior so that grazing is largely manifest as halos radiating from crevices used for daytime shelter (*reviewed by* Andrew & Byrne 2001). Typical of the Tasmanian east coast, the incipient *C. rodgersii* barrens investigated occurred deeper than 8 m where a combination of wave action and mechanical abrasion by macroalgae appears to determine the shallow limit of the barrens (Johnson et al. 2005) and also passage by urchins between neighbouring patches.

The temporal response of the algal community following *C. rodgersii* removal was assessed using a non-destructive spatially nested sampling design consisting of 3 replicate incipient barrens patches within each treatment (removal vs. unmanipulated control), and 4 replicate quadrats (0.25 m^2) haphazardly sampled within each patch on each sampling occasion. Manipulations commenced in spring 2003 (19th November) with a single pair of barren patches (9-10 m depth) randomly assigned as either urchin removal or unmanipulated control. The 4 additional barrens patches (~150 m from original site in slightly deeper water 14-15 m depth) were discovered four months later. To reduce possible bias of seasonal variability in algal recruitment on algal recovery, the additional barrens patches were manipulated during the following spring 2004 (24th November). These patches were monitored over the preceding 8 months prior to random assignment of the urchin removal treatment to two of the patches. Thus, there was a total of 3 replicate urchin removal and 3 replicate control patches. Treatments were maintained and patches sampled every ~2 months over ca. 36 mo. The response of canopy-forming algal species was of *a priori* interest and comparison among treatments was planned at 6, 12 and 24 months post removal of *C. rodgersii*.

Reflecting the spatially circumscribed nature of patches, limited movement of adult *C. rodgersii* and apparent low recruitment of juveniles over the duration of the study, there was minimal re-invasion of patches from which urchins had been removed (i.e. <10 individuals were required to be removed during routine maintenance of the urchin removal treatment as compared to a total of 169 urchins removed during the initial application of the treatment). Other large benthic herbivores present on the study reef included the sea urchin *Heliocidaris erythrogramma*, the lucrative blacklip abalone (*Haliotis rubra*) that occurred albeit rarely, and the herbivorous fish *Odax cyanomelas*. In particular, *H. erythrogramma* occurred commonly within barrens patches occupied by *C. rodgersii*; however, this endemic species is not known to form barrens at exposed sites in eastern Tasmania (Johnson et al. 2005). In notable contrast to sea urchin barrens within the historic NSW range, large limpets (> 20 mm) were found to be absent on *C. rodgersii* barrens in eastern Tasmania. Benthic herbivores other than *C. rodgersii* were not manipulated as part of this study.

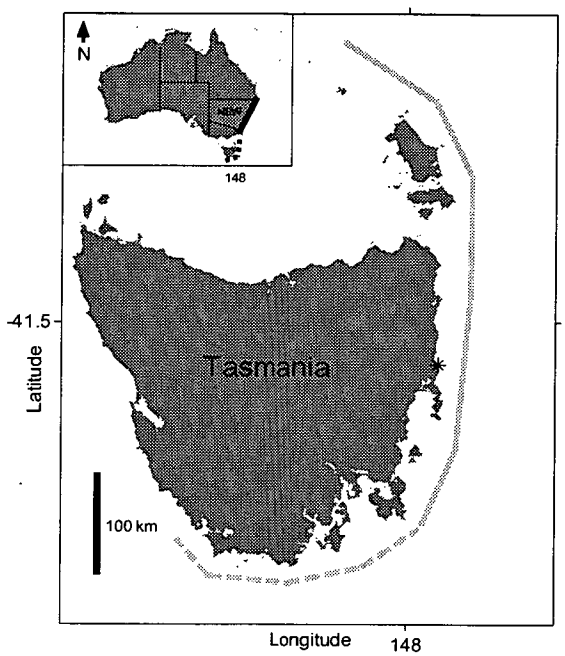

Figure 1. Map of Tasmania showing the experimental site at Bicheno (asterisk). Inset indicates the distribution of *Centrostephanus rodgersii* in south eastern Australia; solid line indicates New South Wales range (*after* Andrew & Byrne 2001); broken line indicates range extension to Tasmania. For main map of Tasmania, solid grey line indicates range over which barrens patches can be found; broken grey line indicates range where individuals, but not barrens patches, have been observed (*after* Johnson et al. 2005; J. Valentine *pers. comm.*).

Monitoring algal response

On each sampling occasion, the 4 replicate 0.25 m^2 quadrats within each experimental patch were photographed to obtain a planar 2-D image of the benthos. Reference to subsurface buoys ensured that sampling occurred only within the original boundaries of the barrens patches. Each quadrat was dissected by a grid of 10 x 10 equidistant lines enabling percentage cover of various taxa (and bare rock) to be estimated from the photographs by enumerating the taxa present at the 100 equidistant points defined by the intersecting lines. Taxa were identified to species where possible; otherwise functional groups were used, *viz.* foliose reds, filamentous reds, filamentous browns, and filamentous green algae. It was difficult to assess cover of non-geniculate coralline algae due to loss of pigmentation in some plants because it was generally unknown whether bleached areas were living or dead. Thus, for the purposes of this study, encrusting coralline algae included both bleached and pigmented components.

Habitat and faunal structure of 'recovered' macroalgal beds – destructive sampling

To assess the impact of *C. rodgersii* barrens on reef structure and associated fauna, all experimental patches were sampled destructively at the end of the experiment after the macroalgal canopy had re-established. On termination of the experiment in November

2006, the original urchin removal patch had experienced 36 months of recovery whereas the additional manipulated patches had experienced 24 months post removal of *C. rodgersii*. Thus, the destructive sampling design at conclusion of the experiment captured both spatially and temporally variable components across patches nested within the urchin removal treatment. To enable comparison of habitat and faunal structure between the urchin removal treatment and adjacent intact macroalgal beds of similar topography (boulder reef) and depth (9-15 m) but unaffected by *C. rodgersii* (i.e. where grazing had not been observed for at least 7 years), the nested experimental design was extended to include 3 adjacent 'intact macroalgal bed' patches. Selected by randomised fin kicks and compass directions, these patches were destructively sampled on termination of the urchin removal experiment. Hence the extended design included 3 levels of 'Treatment' (unmanipulated barrens, sea urchin removal, and unmanipulated intact macroalgal beds), 3 levels of 'Patch' nested within 'Treatment', and 4 quadrats within each 'Patch' providing an estimate of error.

Because the routine photoquadrat monitoring provided only a 2-D representation of the substratum, patterns in total habitat structure (i.e. inclusive of macroalgal canopy, understorey and basal substratum components) were examined in detail at the final assessment by sequentially photographing and then destructively sampling each stratum from top to bottom. The abundance and total length of individual canopy forming macroalga within each quadrat was also measured and the total algal biomass of macroalgal canopy and understorey strata was calculated from dry weights obtained by drying algal samples at 70 °C for 48 hrs. Cover of encrusting and structural invertebrates was estimated from photographs once overlying algae had been removed. Associated benthic fauna was sampled from each quadrat by sealing underwater all excised macroalgal habitat and structural invertebrates in plastic bags, while the remaining benthic fauna were extracted from the substratum using a venturi suction sampler connected to 1 mm mesh bags (each quadrat was systematically suctioned for 3 minutes at a flow rate of 180 $L.min^{-1}$). Fauna contained within algal habitat and/ or benthic suction samples were extracted by thoroughly agitating samples in seawater before passing them through a 1 mm sieve. Faunal samples were then sorted and enumerated at the species level where possible. Where species could not be identified, individual specimens were assigned to taxonomic groups based on the finest taxonomic resolution possible.

Analysis

Univariate analyses

The effects of *C. rodgersii* removal were analysed with a temporal series of 1-way Model III nested ANOVAs of factors 'treatment' (fixed effect) and 'patch nested within treatment' (random effect) at the pre-planned (*a priori*) times of interest of 0, 6, 12 and 24 months post sea urchin removal. Data collected by destructive sampling at the conclusion of the experiment were analysed with the same nested ANOVA structure except for the addition of a third level of treatment, the 'intact macroalgal bed'. All univariate statistical analyses were undertaken using SAS® (v. 6.12) and data were checked for conformity to assumptions of homoscedasticity and normality. Where data were heteroscedastic, the transformation to stabilise variances was determined by the relationship between group standard deviations and means (Draper & Smith 1981). The appropriate transformation for each variable is expressed in terms

of the untransformed variable *Y*. Where lower levels of nesting revealed non-significant results ($P>0.25$, Winer et al. 1991), data at higher levels were pooled *a posteriori* to provide a more powerful test of lower order terms. Multiple range tests were conducting using the Ryan-Einot-Gabriel-Welsch (REGW) procedure. Size-frequency distributions of canopy-forming macroalgae, as assessed at the termination of the experiment, were compared between 'urchin removal' and 'intact macroalgal beds' using the Kolmogorov-Smirnov test.

Multivariate analyses

Comparisons of communities were visualised using nMDS ordination and the species contributing most to dissimilarity were revealed using the SIMPER software routine (PRIMER 5, v5.2.9). Taxonomic diversity of each sample was calculated using the Shannon Diversity Index

$$(H' = -\sum_{i=1}^{s} pi \log_e pi),$$

where *pi* is the proportion of the community that belongs to the *i*th taxa. The significance of differences in assemblage structure was estimated using Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson 2001; Anderson 2005; McArdle & Anderson 2001). All PERMANOVA tests were based on 9999 permutations of Bray-Curtis dissimilarity matrices generated from non-standardised fourth-root transformed data. Significant terms were investigated with *a posteriori* pairwise comparisons using the PERMANOVA t-statistic based on distances of the correct permutable units. Corrections for type-I error rate were made using the Dunn-Sidak method.

Results

Recovery of macroalgal habitat

In all incipient barrens patches from which *C. rodgersii* was removed, a structurally complex assemblage of foliose algae developed that was ultimately dominated by the canopy-forming species *Ecklonia radiata* and *Phyllospora comosa* (Figure 2). Filamentous algae and macroalgal sporophytes (<20 mm height) recruited to available space and began to overgrow the substratum within 1 month of removing the sea urchins. Effects of *C. rodgersii* removal on areal cover of canopy forming macroalgae were statistically detectable at all pre-planned times (~6, 12 and 24 months) after removal of the sea urchin (Table 1). The pattern of re-colonisation for *E. radiata* (by cover) occurred consistently across *C. rodgersii* removal patches, while significant between patch variability was detected for *P. comosa* and total canopy cover (Table 1).

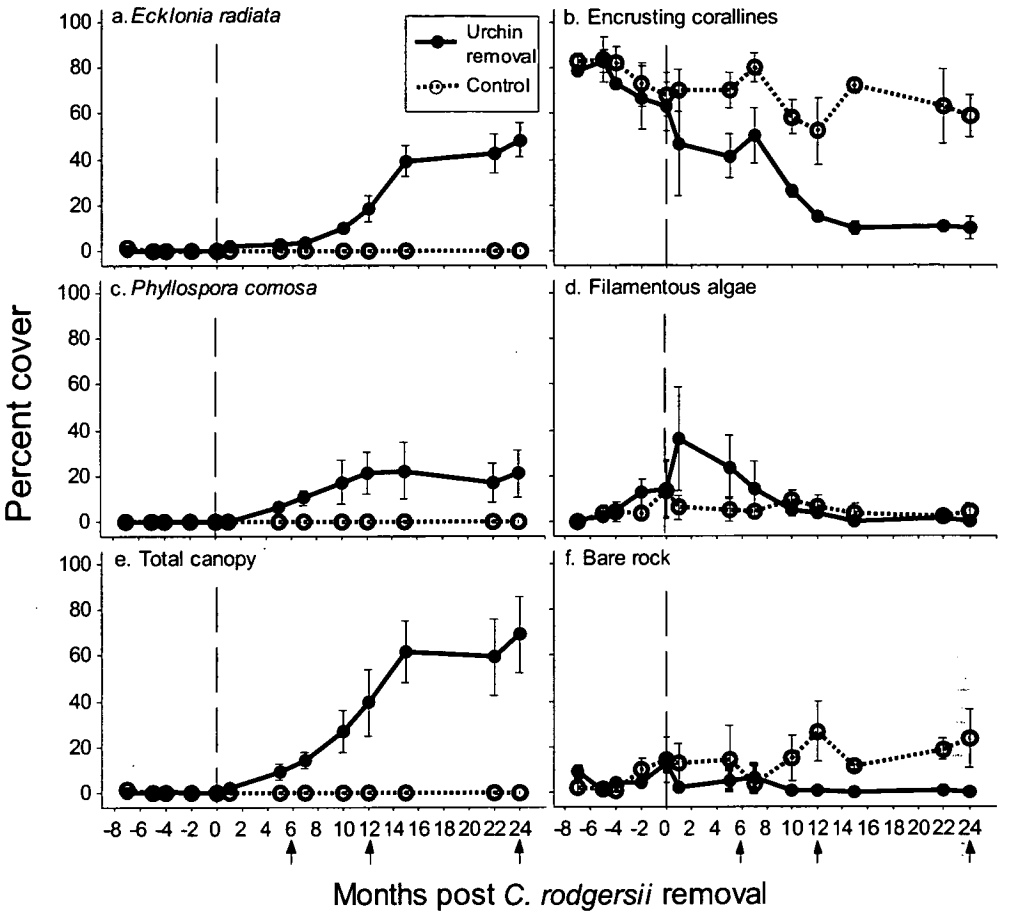

Figure 2. Response of incipient barren patches to removal of *Centrostephanus rodgersii* showing percent cover (mean ± SE) by (a,c,e) canopy-forming macroalgae and (b,d,f) basal substratum layer. Urchin removal treatment (—•—, n=3) and unmanipulated "control" patches (--o--, n=3) are shown. Dashed vertical line in each column shows the timing of urchin removal; negative values on X-axis represent months prior to removals and vertical arrows indicate pre-planned times of interest for analysis of the urchin removal effect. Note: n=2 for months prior to removals.

Assessment of benthic habitat structure by destructive sampling revealed that removal of *C. rodgersii* resulted in replacement of the open barrens substratum with a structurally heterogeneous benthic habitat composed of a macroalgal canopy and accompanying understorey (Figure 3). Nested ANOVA revealed significant differences in both canopy and understorey components between treatment groups with pairwise comparisons revealing differences between urchin removal and unmanipulated barrens, but not between urchin removal and intact macroalgal beds (Figure 3). Patterns in the cover of the basal substratum layer varied between treatment groups (Figure 3), showing consistency across treatments in the cover of encrusting corallines but significantly higher cover of bare rock and filamentous algae on the unmanipulated barrens in comparison to the urchin removal and intact

Table 1. Results of nested model III ANOVA testing effect of *Centrostephanus rodgersii* removal on macroalgal cover at pre-planned months post removal. Significant *P*-values are highlighted in bold face. Note ~6 month sample was only attainable at 7 months post manipulation. Note that prior to applying the *C. rodgersii* removal treatment, no differences in the cover of barrens substratum components were detected between incipient patches (encrusting corallines, $F_{1,4}$=0.1200, P=0.7418; bare rock [trans.=$Y^{0.22}$], $F_{1,4}$=0.1247, P=0.8030; filamentous algae, $F_{1,4}$=0.01 P=0.9460).

Response variable [transformation 6mo; 12mo; 24mo]	Source	Orthogonal pre-planned comparisons		
		T~ 6 mo	T= 12 mo	T= 24 mo
Ecklonia radiata [log(Y+0.0001), $Y^{0.28}$, $Y^{0.24}$]	Treatment	$F_{1,22}$=53.15	$F_{1,4}$=33.97	$F_{1,22}$=80.22
		P<0.0001	**P=0.0043**	**P<0.0001**
	Patch(Treatment)	$F_{4,18}$=0.54	$F_{4,18}$=2.28	$F_{4,18}$=0.51
		P=0.7070	P=0.1006	P=0.7317
Phyllospora comosa [log(Y+0.0001) ; $Y^{0.45}$; log(Y+0.0001	Treatment	$F_{1,4}$=585.85	F=7.87	$F_{1,22}$=33.34
		P<0.0001	**P=0.0485**	**P<0.0001**
	Patch(Treatment)	$F_{4,18}$=5.19	$F_{4,18}$=10.07	$F_{4,18}$=0.68
		P=0.0059	**P=0.0002**	P=0.6133
Total canopy macroalgae [, $Y^{0.67}$,]	Treatment	$F_{1,4}$=14.08	$F_{1,4}$=10.07	$F_{1,4}$=17.21
		P=0.0199	**P=0.0338**	**P=0.0143**
	Patch(Treatment)	$F_{4,18}$=5.89	$F_{4,18}$=9.45	$F_{4,18}$=15.35
		P=0.0033	**P=0.0003**	**P<0.0001**

macroalgal treatments. Canopy-forming macroalgae occurred at higher abundance within the urchin removal treatment than on barrens habitat or intact macroalgal beds, whereas in barrens patches there were low numbers of minute (<50 mm length) individuals, macroalgae in the urchin removal patches were dominated by small individuals tailing to large size classes, and in the intact macroalgal habitat, there were fewer but relatively more larger individuals (Figure 4). Comparison of macroalgal size-frequency between urchin removal and intact macroalgal beds revealed significantly different size distributions (Kolmogorov-Smirnoff, P< 0.0001). For urchin removal patches, total algal biomass m^{-2} (canopy plus understorey species, excluding encrusting corallines) was not statistically different to that of intact macroalgal beds but was much greater than for the barrens habitat (total algal biomass for urchin removal patches = 845.68 $g.m^{-2}$ ± 451.81 SE; intact macroalgal beds = 844.22 $g.m^{-2}$ ± 127.45 SE; unmanipulated barrens = 0.20 $g.m^{-2}$ ± 0.04 SE, nested model III ANOVA; trans.=(log(Y+0.0001), Treatment, $F_{(2,6)}$=84.07, P<0.0001; Patch(Treatment), $F_{(6,27)}$=1.98, P=0.1035). Other benthic structural components, namely sessile encrusting and erect invertebrates, contributed to the physical structure of recovered macroalgal and intact macroalgal habitats, but contributed little to barrens (Figure 5).

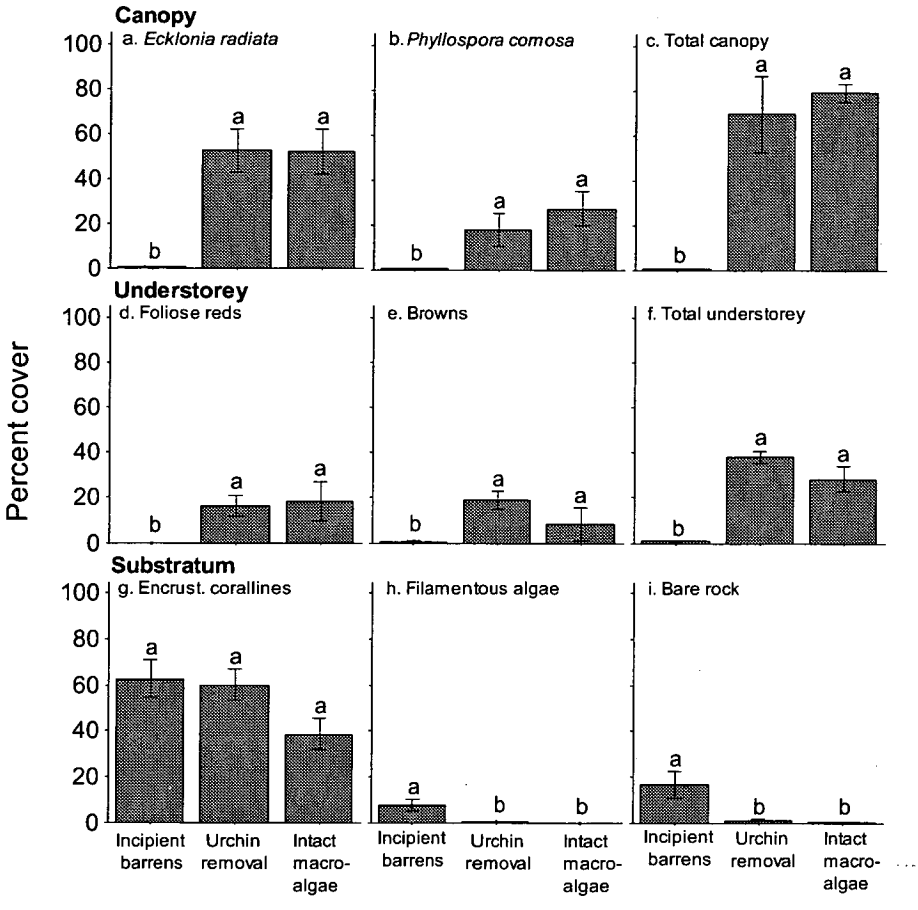

Figure 3. Percent cover (mean ± SE) of unmanipulated barrens (incipient barrens), barrens with urchin removal, and intact macroalgal beds for (a,b,c) canopy, (d,e,f) understorey and (g,h,i) substratum components of benthic habitat structure. Bars with identical letters indicate Ryan-Einot-Gabriel-Welsch (REGW) groupings of treatments for each response variable, α=0.05

Effect of barrens on taxonomic diversity

Recovery of canopy-forming macroalgae within *C. rodgersii* removal patches (Figure 6A) resulted in an associated re-colonisation of this habitat by a benthic faunal assemblage vastly different to the barrens, but not different to that observed in intact macroalgal beds (Figure 6B; see Table 2 for PERMANOVA summaries). Removing *C. rodgersii* clearly increased taxonomic richness, total abundance and Shannon diversity of benthic fauna (independent of structure-forming invertebrates); however, there was little difference in the composition of benthic faunal communities between urchin removal and intact macroalgal bed treatments (Figure 7).

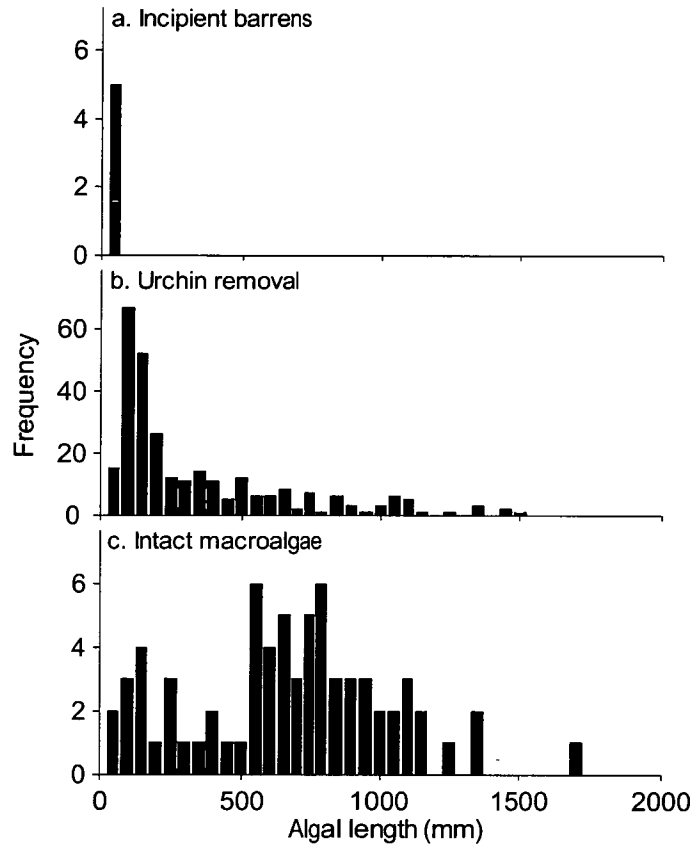

Figure 4. Size-frequency distributions of canopy-forming macroalgal species (*Ecklonia radiata* and *Phyllospora comosa*) at termination of the experiment in a. incipient barrens patches (n=5), b. *Centrostephanus rodgersii* removal patches (n=287), c. intact macroalgal beds (n=70). Note different scales for Y-axes.

The taxa contributing most to dissimilarity in faunal abundance between macroalgal bed and barrens habitats were Amphipoda 38.2 %; Polychaeta 8.76 %; Isopoda 6.91 %; Gastropoda 6.16 %; Tanaidacea 3.95 %; Hirudinea 3.59 %; Bivalvia 3.47 %; Echinodermata 3.06 %; Mysidaceae 2.66 %; Serpulidae 2.65 %; Decapoda 2.05 %; Brachiopoda 1.80 %; Terebellidae 1.68 %; and Oligochaeta 1.51 %. Graphical examination of whole benthic communities (flora and fauna), based on presence/ absence of all described taxa (including structure-forming invertebrates) revealed overwhelmingly different benthic communities in the presence of *C. rodgersii* grazing (Figure 6C; see Table 2 for PERMANOVA summary). Of the 296 individual floral and faunal taxa recorded, only 72 were present within incipient barrens, 253 in the urchin removal patches, and 221 within intact macroalgal beds (*see* Appendix I). Thus, formation of barrens by *C. rodgersii* is estimated to result in a minimum localised loss of ~150 taxa associated with eastern Tasmanian macroalgal beds.

Discussion

Effect of sea urchin range expansion on reef habitat

Climate change is leading to re-distribution of marine species and altering ecosystem dynamics (e.g. Harley et al. 2006; Rosenzweig et al. 2007). Within the newly extended eastern Tasmanian range of *Centrostephanus rodgersii*, this sea urchin now deconstructs macroalgal habitat and maintains a simplistic and homogeneous benthic habitat typical of barrens described from its endemic range (e.g. Andrew & Byrne 2001) and broadly typical of sea urchin 'coralline' barrens throughout the world (*reviewed by* Pinnegar et al. 2000). Removal of *C. rodgersii* from barrens patches in eastern Tasmania resulted in a rapid replacement of the flat structurally homogeneous substratum of the initial urchin barrens with a structurally heterogeneous 3-dimensional benthic habitat complete with macroalgal canopy, diverse algal understorey and structural basal invertebrates. Indeed the dramatic and consistent pattern of algal recovery across all urchin removal patches indicated that the timing of urchin removals from barrens patches (September 2003 as opposed to September 2004) was unimportant. While patterns in canopy cover and algal biomass clearly converged on that observed for intact macroalgal beds, recovering patches were still biased towards smaller and yet more abundant plants indicating that effects of previous grazing on community succession were still detectable >24 months after removal of the sea urchin. Most importantly, however, return to the macroalgal-dominated ecosystem state (macroalgal canopy cover >50 %) was achieved rapidly (within ca. 15 months) after urchin removal (for comparison of algal recovery in other systems *see* Duggins 1980; Himmelman et al. 1983; Keats et al. 1990; Johnson & Mann 1993; Leinass & Christie 1996).

In contrast to the rapid and consistent pattern of macroalgal recovery observed in the current study, experimental removals of *C. rodgersii* in NSW result in less predictable transition to assemblages of foliose algae and often slower or less complete recovery of canopy-forming species, a result consistently attributed to patterns in propagule supply (Fletcher 1987; Andrew 1991; Andrew 1993; Andrew et al. 1998; Hill et al. 2003). Indeed a notable difference in the barrens assemblage across eastern Tasmania is the general lack of limpet "mesograzers" that occur in high abundances on *C. rodgersii* barrens in NSW and are capable of delaying macroalgal recovery following *C. rodgersii* removal (Fletcher 1987). Thus the functional redundancy of the grazer group on barrens throughout eastern Tasmania would likely be enhanced if limpets were to establish at high densities. While regional differences in macroalgal growth rates and grazer interactions are likely, experiments on NSW reefs were generally undertaken on, or near, widespread barrens habitat. Conversely, I manipulated small incipient barrens patches (scale of metres) surrounded by reef dominated by dense macroalgal habitat, which likely provided a saturating supply of algal propagules at this scale. Therefore, direct scaling–up of these results is likely to lead to over-expectations of macroalgal recovery rates for larger scale barrens (10^2-10^3 m) where algal propagule supply may become limiting (*reviewed by* Dayton 1985). Unlike the dynamic recovery of macroalgal habitat following *C. rodgersii* removal, un-manipulated barrens patches displayed high stability over the 3-year duration of the study. In combination with *in situ* observations at several sites over > 8 years (pers. obs.), *C. rodgersii* barrens in eastern Tasmania appear to constitute a truly alternative and persistent state as also reported for conspecific barrens in NSW (*reviewed by* Andrew & Byrne 2001).

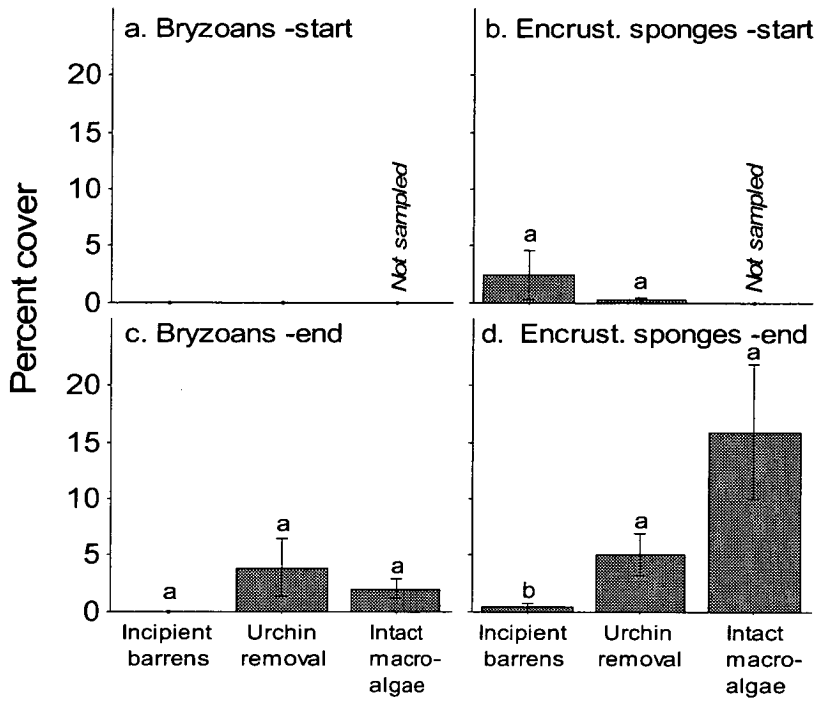

Figure 5. Effect of *Centrostephanus rodgersii* on the cover of (a,c) habitat forming bryzoans and (b,d) encrusting sponges for incipient barrens, urchin removal, and intact macroalgal patches. Start of experiment prior to sea urchin removal, bryzoans absent; sponge cover (nested model III ANOVA; trans.=$Y^{0.69}$, 'Treatment', $F_{(1,5)}$=1.09, P=0.3548; 'Patch(Treatment)', $F_{(4,18)}$=24.09, P<0.0001). End of experiment, bryzoans (trans.= log(Y+0.0001), 'Treatment', $F_{(2,6)}$=3.23, P=0.1116; 'Patch(Treatment)', $F_{(6,27)}$=6.02, P=0.0004); sponges (nested model III ANOVA; trans.=log(Y+0.0001), 'Treatment', $F_{(2,33)}$=11.05, P=0.0002; 'Patch(Treatment)', $F_{(6,27)}$=0.85, P=0.5423). Bars with identical letters indicate REGW groupings of treatments within each sampling period, α=0.05.

Effect of sea urchin grazing on taxonomic diversity within the expanded range

Examination of the benthic fauna in barrens patches confirmed major effects of *C. rodgersii* grazing that extend to the entire benthic community. While *C. rodgersii* is known to be omnivorous, consuming encrusting and structure-forming invertebrates as well as algae (A. Pile *pers. comm.*; Author *pers. obs.*), the greatest faunal impacts by *C. rodgersii* appear to be those caused by loss of macroalgal habitat due to intense herbivory. Indeed, the barrens state is characterised by an impoverished benthic community, with ~150 taxa fewer than adjacent macroalgal beds (*also see* Himmelman et al. 1983; Bodkin 1988; Graham 2004). By considering the potential number of species either directly consumed by sea urchins or those simply associated with macroalgal habitat (e.g. Graham 2004), the total number of taxa potentially impacted by *C. rodgersii* grazing in eastern Tasmania may increase dramatically. As an example,

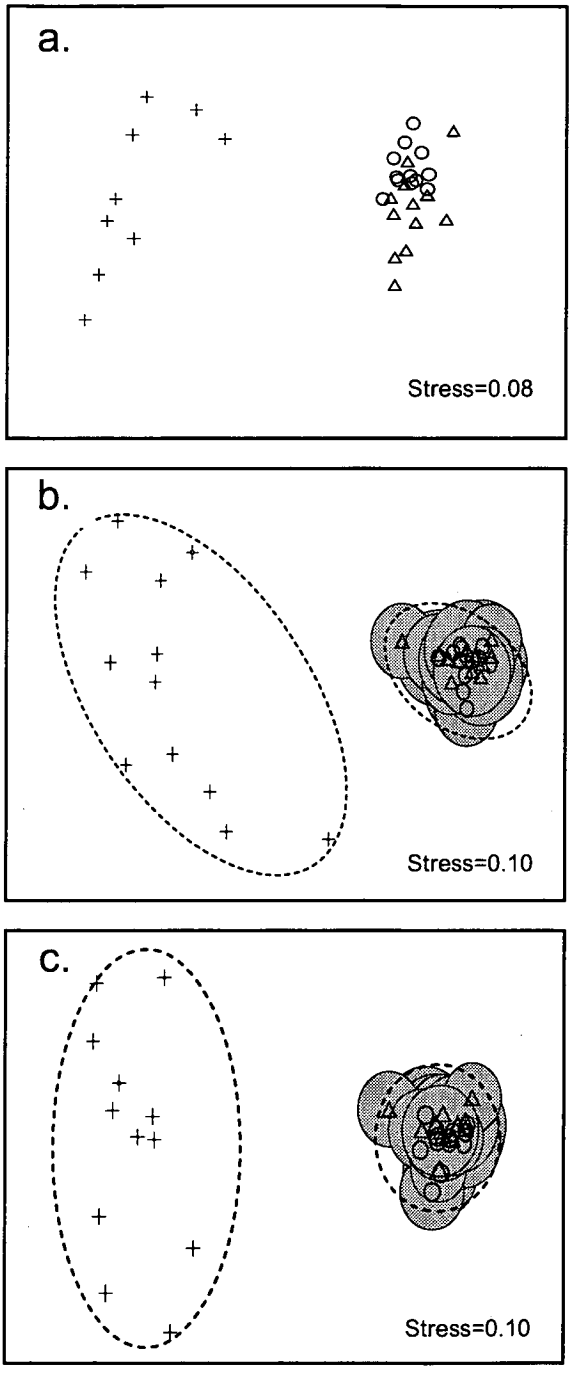

Figure 6. Ordinations (nMDS) showing the effect of *Centrostephanus rodgersii* on (a) benthic algal assemblages; (b) benthic faunal assemblages; and (c) entire benthic assemblages (flora plus fauna) at termination of experiment. Symbols represent individual quadrats nested within replicate barrens patches (crosses), urchin removal patches (triangles), and intact macroalgal beds (circles). Ordinations are based on Bray-Curtis similarity matrices obtained from fourth-root transformed percent cover data for algae; abundance data for faunal assemblages; and presence/ absence data for whole benthic assemblages. Faunal and whole assemblage ordinations are overlaid with a bubbleplot (grey) representing macroalgal canopy cover (largest bubbles represent 100% macroalgal canopy cover); dashed ellipses encompass space occupied by the alternative assemblages of barrens and macroalgal ecosystem states.

intensive grazing by *C. rodgersii* eliminates almost all algal species of which there are an estimated 373 species in Tasmanian coastal waters alone (*reviewed by* Sanderson 1997). Thus, one may expect that the rate of species accumulation with increasing sampling area (the species-area curve) is likely to be much greater for heterogeneous macroalgal habitat relative to homogenous barrens were a consistent community containing relatively few species is observed.

In a similar study by Vance (1979) in California, overgrazing of macroalgal habitat by the congeneric *Centrostephanus coronatus* also dramatically decreased local taxonomic diversity. Interestingly, the author considered that a patchwork of grazed patches among macroalgal habitat may have the net effect of increasing diversity of the community as a whole because localised barrens patches may provide habitat for grazer resistant taxa that were otherwise rarely observed. While there were few taxa (< 6) unique to barrens patches studied in eastern Tasmania (other than *C. rodgersii* itself, *see* Appendix I), clearly, it is the catastrophic shift to widespread barrens (10^2–10^3 m), via the coalescence of incipient barrens patches, that will lead to loss of taxonomic diversity across increasingly large and ecologically important spatial scales. Furthermore, formation of *C. rodgersii* barrens may also be expected to result in negative impacts for nektonic species that associate with macroalgal habitat either as a result of direct habitat loss or loss of an abundance of prey items associated with vegetated habitats (e.g. Edgar & Shaw 1995).

Table 2. PERMANOVA testing the effect of *Centrostephanus rodgersii* on algal, faunal and entire benthic assemblages at conclusion of the experiment. Results are (I) 1-way mixed model nested PERMANOVA; (II) tests among treatments; and (III) dissimilarities within and between treatments. For pair-wise tests, Monte Carlo (MC) asymptotic *P*-values were used given the small number of unique permutations (*after* Anderson 2005). Significant values shown in bold face, note pair-wise *a posteriori* comparisons were made after adjusting the type I error rate, α=0.017.

I. PERMANOVA		**Algal assemblage**		**Faunal assemblage**		**Whole benthic assemblage**	
Source	***df***	***F***	***P*(perm)**	***F***	***P*(perm)**	***F***	***P*(perm)**
Treatment	2	15.87	**0.0129**	6.41	**0.0096**	7.33	**0.0076**
Patch(Treatment)	6	2.76	**0.0071**	1.69	**0.0130**	1.70	**0.0186**
Residual	27						
Total	35						
II. Tests among 'Treatment'							
Groups	**unique perm.**	***t***	***P*(MC)**	***t***	***P*(MC)**	***t***	***P*(MC)**
Barrens vs Removal	10	4.46	**0.0015**	2.80	**0.0097**	3.02	**0.0055**
Barrens vs Intact	10	5.34	**0.0009**	2.71	**0.0098**	2.93	**0.0081**
Removal vs Intact	10	1.02	0.3996	1.12	0.3170	1.13	0.3207

III. Average Bray-Curtis % dissimilarities within and between treatments: macroalgal; faunal; whole assemblages

	Barrens	Removal	Intact
Barrens	21.88; 46.98; 43.90		
Removal	64.85; 69.48; 67.95	25.38; 25.00; 23.72	
Intact	65.31; 68.92; 68.44	21.06; 27.05; 26.32	18.21; 27.21; 26.69

While the spatial grain of the current study was considered too small for adequate examination of effects of *C. rodgersii* barrens on fish assemblages (reef fish in Tasmania typically possess home ranges >2000m^2, Barrett 1995), of the few small cryptic fishes (<100 mm length) sampled from the benthos (a total of 15 individuals in 7 taxonomic groups), none were recorded from the barrens.

Effects of barrens on ecosystem functioning

As evidenced by the dramatic recovery of standing stocks in algal biomass and associated benthic fauna, vast change in physical and community structure of rocky reefs occurs with the transition from macroalgal beds to *C. rodgersii* barrens. What remains less clear is how such shifts impact ecosystem functioning. However, given that epifauna are known to be major contributors to the flux of materials in macroalgal dominated reef habitats (e.g. Taylor 1998), the loss of fauna on barrens implies major functional differences between alternative macroalgal and barrens states. Ultimately,

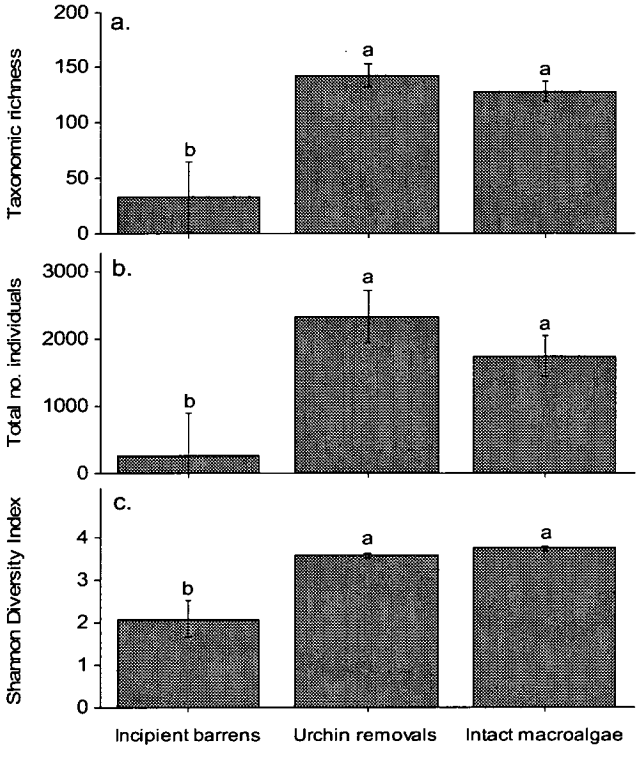

Figure 7. Effect of *Centrostephanus rodgersii* on benthic faunal diversity assessed at the end of the experiment on incipient barren patches, urchin removal patches and intact macroalgal beds. Data shown are means per m^2 ± SE and do not include habitat-forming invertebrates. a. Taxonomic richness, i.e. total number of taxa (Model III 1-way nested ANOVA; trans.=$Y^{0.5}$, Treatment, $F_{(2,6)}$=125.47, P<0.0001; Patch(Treatment), $F_{(6,27)}$=1.71, P=0.1575). b. Total number of individuals (trans.=$Y^{0.22}$, Treatment, $F_{(2,27)}$=57.45, P<0.0001; Patch(Treatment), $F_{(6,27)}$=1.34, P=0.2728). c. Shannon diversity index (Treatment, $F_{(2,33)}$=123.42, P<0.0001; Patch(Treatment), $F_{(6,27)}$=0.56, P=0.7589), note index was calculated using $\log_e$. Bars with identical letters indicate REGW groupings, α=0.05.

the conversion of macroalgal beds to widespread *C. rodgersii* barrens within the extended Tasmanian range is anticipated to reduce benthic primary (*after* Chapman 1981; Babcock et al. 1999) and secondary productivity (e.g. Duggins et al. 1989), with flow-on effects to many species including species of commercial importance (Andrew & Underwood 1992; Andrew et al. 1998; Johnson et al. 2005).

Habitat loss coupled with changing climate

These results demonstrate that disproportionately large impacts on marine biodiversity may occur as a result of range shifts of key habitat-modifying organisms. Furthermore, climate change also acts independently on individual species within a community (e.g. Parmesan & Yohe 2003). Thus, loss of local habitat as a result of range extension by habitat-modifying organisms, coupled with large scale shifts in the suitable 'climate envelope' (e.g. Hijmans & Graham 2006), may be particularly devastating for some populations, particularly those with contracted ranges to begin with. These kinds of interactions are acutely relevant in places like Tasmania where poleward range retreat is prevented by a lack of contiguous poleward land mass. Indeed, large-scale decline of the giant kelp *Macrocystis pyrifera* in eastern Tasmania over the past 50 years appears to be the result of the new regime of warm, nutrient-poor water on this coast (e.g. Edgar et al. 2005; *see also* Ridgway 2007). While *C. rodgersii* grazing does not appear responsible for decline of this macroalga over large scales, localised barrens formation may prevent recovery of this alga at some sites even if poor nutrient conditions for plant growth were temporally reversed. Moreover, because further strengthening of the EAC and greater thermal stratification are predicted for south eastern Australia under global climate change (Cai et al. 2005), coastal waters off eastern Tasmania appear committed to a warm and oligotrophic trajectory (*reviewed by* Poloczanska et al. 2007). This trend will have a positive effect on the reproductive success of *C. rodgersii* (Ling et al. 2008, *see* Chapter 2) but will negatively influence macroalgal growth and likely result in more frequent dieback events (e.g. Valentine & Johnson 2004). Thus the warming climate of this coast appears poised to tilt macroalgal-urchin dynamics in favour of further sea urchin grazing and disproportionately large effects on reef biodiversity.

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CHAPTER 5: POPULATION DYNAMICS OF AN ECOLOGICALLY IMPORTANT RANGE EXTENDER: BARRENS-FORMING VERSUS BARRENS-MAINTAINING SEA URCHINS

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Abstract

The barrens-forming sea urchin *Centrostephanus rodgersii* (Diadematidae) has recently undergone poleward range-extension to eastern Tasmania where grazing of diverse and economically important macroalgal beds has occurred. We compare growth, biometric, dietary and morphometric characteristics of *C. rodgersii* between macroalgal habitat and adjacent barrens to inform population dynamics of the sea urchin within the newly extended range. The age structure of *C. rodgersii* in macroalgal habitat and adjacent barrens is similar, suggesting that both habitats have been influenced by similar recruitment events. However, there are clear differences in the body size, body mass, spine length and diet of sea urchins in the two habitat types. We identify two broad morphologies of *C. rodgersii*; one of relatively large size with thick test, rapid growth and short-spines that persists and grazes macroalgal beds (barrens-forming eco-morph). The other eco-morph persists on the barrens habitat and demonstrates smaller body size, slower growth, thinner test, gut contents of closely cropped filamentous-coralline algae and only occasionally fleshy macroalgae; but occurs at higher density, possesses longer spines and appears to enhance the persistence stability of barrens habitat once formed (i.e. barrens-maintaining eco-morph). Invading dense, swell prone macroalgal habitat of eastern Tasmania, the phenotypic plasticity displayed by this sea urchin appears to be an important mechanism facilitating colonisation of reef habitats within the extension-region. Importantly, habitat-specific patterns in population dynamics are broadly consistent with that observed from within the historical range, suggesting that patterns in macroalgal-sea urchin dynamics and the ecological importance of this species will be similar across the newly extended range.

Introduction

Climate change is predicted to have major impacts on the distribution of species in the worlds' oceans (Rosenzweig et al. 2007). As oceans warm, a re-shuffling of species distributions towards the poles (e.g. Walther et al. 2002; Parmesan & Yohe 2003) will lead to changes in biological interactions which may lead to major shifts in coastal ecosystems, particularly if ecologically dominant species undergo range modification (e.g. Hughes 2000; Harley et al. 2006). While many species are known to play dominant functional roles in particular coastal ecosystems (e.g. Andrew & Byrne 2001; Steneck et al. 2002; Micheli & Halpern 2005), the dynamics of such species and their ecological significance at higher latitudes is speculative. While species-specific and or regional idiosyncrasies are likely, understanding the population dynamics and function of such species within new ranges will be essential to anticipate broader ecosystem responses.

Driven by a changing regional climate, the diadematid sea urchin *Centrostephanus rodgersii* (Agassiz) has undergone recent poleward (southern) range extension from south east mainland Australia to Tasmania (Johnson et al. 2005; Ling et al. 2008; *see* Chapters 2&3). Invading dense and productive macroalgal beds, incursion of *C. rodgersii* in Tasmania is important given the species' ability to catastrophically overgraze algal dominated habitat, which results in widespread and persistent sea urchin barrens throughout the species historical New South Wales (NSW) range (*reviewed by* Andrew & Byrne 2001; *see* Figure 1). Indeed, such is the dominant ecological effect of *C. rodgersii* that within its historical range the sea urchin has formed and maintains barrens over approximately 50% of all near-shore rocky reefs (Andrew & O'Neill 2000).

Since first detected on the Tasmanian mainland coast in 1978, the sea urchin's abundance has increased and evidence of barren areas now occur in some Tasmanian locations (Johnson et al. 2005). The potential for broad-scale ecological shift from luxuriant macroalgal beds to sea urchin barrens in Tasmania therefore poses a major threat to local biodiversity and valuable reef based fisheries that depend on macroalgal beds (Johnson et al. 2005; Ling 2008). Hence, understanding characteristics of *C. rodgersii* populations leading to barrens formation and the expression of such characters on reefs within the extension-region is therefore important in assessing the ecological role of this sea urchin within Tasmania.

From studies in NSW, it is clear that a threshold density of *C. rodgersii* is required to initiate widespread destructive grazing of macroalgae, and that this density is greater than that necessary to maintain barrens (Andrew & Underwood 1993; Hill et al. 2003). As typical among diadematids, *C. rodgersii* is nocturnal and displays a homing behavior so that localized grazed patches are manifest as halos radiating from crevices used for daytime shelter (*reviewed by* Andrew & Byrne 2001). Importantly, the 'catastrophic shift' (*after* Scheffer et al. 2001) from small grazed patches (<1-10s m) to widespread barrens (100s m) occurs when localized grazed patches coalesce (Andrew 1993; Andrew & Underwood 1993; Hill et al. 2003). Thus, *C. rodgersii* forms barrens in a different way to that documented for most other sea urchins (e.g.

Strongylocentrotid species), which typically aggregate to form highly destructive mobile feeding fronts (e.g. Lang & Mann 1976; Lauzon-Guay & Scheibling 2007). Although the predominant mode of *C. rodgersii* barrens formation hinges on the use of localised shelter (a feature that makes barrens formation by this species highly predictable) populations maintaining widespread barrens in NSW and Tasmania do occur on featureless flat-rock habitat, indicating that shelter is not obligatory for *C. rodgersii* to form barrens (Andrew 1993; Andrew & Byrne 2001; Johnson et al. 2005).

While widespread barrens currently occur in relatively few places in eastern Tasmania, the major feature of *C. rodgersii* grazing this coast is the occurrence of small barrens patches within dense macroalgal beds, a condition referred to as incipient barrens (Johnson et al. 2005). Indeed, widespread barrens are currently only observed in north eastern Tasmania (including the Kent Group in eastern Bass Strait), while incipient barrens can be found across the east coast but have not been reported in southern Tasmania where the sea urchin is rare and only occurs as scattered individuals (Johnson et al. 2005; *see* Figure 1). Within the NSW range, boundaries between *C. rodgersii* barrens and macroalgal habitat demonstrate high stability and often align with discontinuities in reef substratum type or interactions with the sweeping motion of large brown seaweeds that can create an abrasive 'whiplash' effect on the benthos that appears to restrict the distribution of the sea urchin (e.g. Andrew 1993; see *review by* Andrew & Byrne 2001; *also see* Konar 2000). However, such a pattern of stability between macroalgal boundaries and barrens habitat does not account for many sites in Tasmania where grazed patches display sharp boundaries on reefs with otherwise continuous rocky substrata. Furthermore, grazed areas on Tasmanian reefs are currently observed in relatively deep water (>10 m depth) (Johnson et al. 2005) compared to that observed within the historic range of *C. rodgersii* where the barrens habitat extends across relatively shallow reefs (<5 m depths) (Andrew & Byrne 2001).

The recent nature of the *C. rodgersii* range-extension and an increasing occurrence of grazing in Tasmania suggests that the sea urchin may have the capability to form widespread barrens over much of this coastline (Johnson et al. 2005). Clearly, the potential for expansion of *C. rodgersii* barrens in Tasmania, either by grazing at the edges of recently formed barrens or coalescence of smaller incipient barrens patches, is dependent on the dynamics of sea urchins at the boundaries of macroalgal habitat coupled with the dynamics of individuals maintaining previously grazed areas. Because demographic transitions of sea urchin populations may inform the dynamics of overgrazing (e.g. Lang & Mann 1976; Kenner 1992; Pederson & Johnson 2008), we investigate population dynamics of *C. rodgersii* within the extension-region by comparing the growth, biometric, dietary and morphometric characteristics of sea urchins on recently formed barrens with those existing within macroalgal boundaries. Observed dynamics are discussed with respect to well documented patterns from within the species historic range.

Materials and Methods

Study sites

We conducted the research in north eastern Tasmania at St. Helens where there are recently formed *Centrostephanus rodgersii* barrens and transitional zones between barrens and macroalgal beds (*hereafter the* "macroalgal boundary habitat"). Further south, *C. rodgersii* inhabiting incipient barrens were examined at 3 sites, *viz.* Freycinet Peninsula, Maria Island and Tasman Peninsula (Figure 1). At St. Helens, the average density of *C. rodgersii* on barrens (2.09 ± 0.1 SE m^{-2}; 10-20 m depth) was higher than that within adjacent macroalgal boundary habitat (1.61 ± 0.2 SE m^{-2}; 8-12 m depth) or that within the interior of macroalgal beds where density declined rapidly (0.36 ± 0.2 SE m^{-2}; 8-20 m depth). For incipient barrens patches at the 3 other sites (15-20 m depth), average *C. rodgersii* density within patches ranged from ~1.5-3 m^{-2}. As observed in some parts of the sea urchins NSW range, subtidal macroalgal beds on the exposed eastern Tasmanian coast are dominated by *Phyllospora comosa* (Seirococcaceae) (~3-15 m depth) and/ or *Ecklonia radiata* (Laminariales) (~8–20 m depth) that typically form an algal canopy reaching ~1-2 m in height from the reef surface.

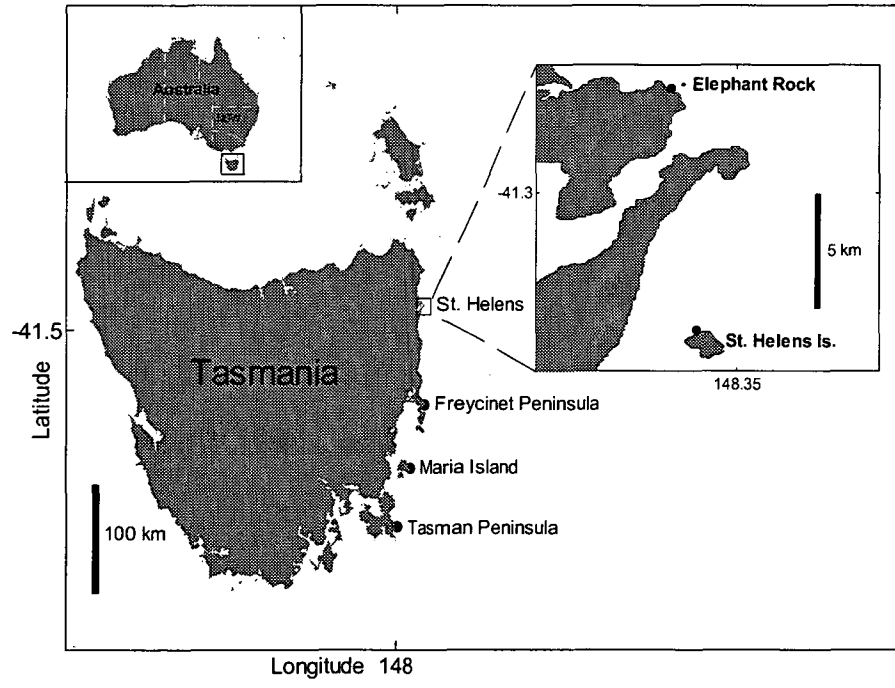

Figure 1. Location of study sites in Tasmania, south eastern Australia. At both sites near St. Helens, *Centrostephanus rodgersii* was sampled from recently formed barrens and adjacent macroalgal boundary habitat. The three sites further south are where *C. rodgersii* was sampled from incipient barrens.

Growth, size and age structure

Habitat-specific growth models were derived by analysis of annual growth increments of tagged sea urchins. Sea urchin age-structure was then estimated for each habitat using the growth models to predict age-at-size for large numbers of individuals (n=300). Individuals were tagged with tetracycline and growth increment data obtained from the change in length of jaw structures (demipyramids). Because demi-pyramids (jaws) of sea urchins grow continuously throughout a sea urchins lifetime and the growing edge stains readily with tetracycline, sea urchin jaws provide a suitable structure to assess growth under field conditions (*after* Ebert 2001, 2004; Pederson & Johnson 2008). For each of two sites near St. Helens (Figure 1), sea urchins ranging from 61 – 133 mm test diameter (TD) were obtained from recently formed barrens habitats and adjacent macroalgal boundary habitat by divers thoroughly searching and collecting all urchins from a randomly positioned plot (approximately 8 by 8 m) within each habitat until approximately 300 individuals were obtained. At the surface, each individual was tagged by injection of 2–4 ml (depending on size) of tetracycline-HCL (conc. 20 gL^{-1} seawater) through the peristomial membrane. This dosage provided consistently readable tags in pilot field trials. Tagged urchins were returned promptly to the permanently marked experimental plots and allowed to grow for at least 12 months before attempts to recover tagged individuals were made by collecting all sea urchins from within the plots and to 5 m outside their boundary (Table 1).

Table 1. Summary of *Centrostephanus rodgersii* tetracycline tagging in barrens and macroalgal boundary habitat at St. Helens, 2004-2005. Growth models were generated from growth increment data standardised at 365 days growth.

Habitat	Site	No. tagged	Date of Tagging	Date of Recovery	Days at liberty	Urchins collected	Tags recovered
Macroalgal boundary	Elephant Rock	341	28/07/04	22/09/05	421	731	153
Macroalgal boundary	St. Helens Is.	383	17/08/04	11/10/05	420	660	89
Barren	Elephant Rock	315	26/07/04	28/07/05	367	654	101
Barren	St. Helens Is.	283	29/07/04	29/07/05	365	679	74
Total		1322				2724	417

Preparation of jaws and measurement of growth increments

Prior to removing jaw structures, the test diameter of each individual was measured using knife edge vernier callipers. The complete Aristotle's lantern was removed, labelled and soaked in 12.5 % sodium hypochlorite for 48 hrs to dissolve connective tissue and expose individual jaw structures that were then dried and checked under UV light for the presence of a fluorescing tetracycline tag. For each tagged individual, a jaw growth increment (ΔL) was estimated by measuring (to 0.05 mm) the distance from the inside edge of the fluorescing band to the growing aboral edge of the jaw with an ocular micrometer under 20x magnification. Jaw length at time of recapture ($L_{t+\Delta t}$)

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was measured (to 0.1 mm) using knife edge vernier callipers. Estimated jaw length at time of tagging (L_t) was calculated by subtracting the growth increment (ΔL) from jaw length at time of recapture ($L_{t+\Delta t}$ - ΔL).

Selection and fitting of growth models

For tag-recaptured *C. rodgersii* in eastern Tasmania, the pattern of annual jaw growth increment (ΔL) versus initial jaw size at tagging (L_t) indicated an indeterminate growth pattern best described by an inverse logistic function. Optimum fits for the inverse logistic functions were determined by minimising the sum of the negative log-likelihoods for each of the observed growth increments (ΔL) and the expected growth increments derived by the model. The expected variation around the growth increments was explicitly modelled as a power function of the expected length (*see* Haddon et al. 2008). The inverse logistic equation is written as:

$$\Delta L = \frac{Max\Delta L \times \Delta_t}{1 + e^{Ln(19)\frac{\left(L_t - L^m_{50}\right)}{\left(L^m_{95} - L^m_{50}\right)}}} + \varepsilon_{L_t} \qquad \text{(eqn. 1)}$$

Where $Max\Delta L$ is the hypothetical asymptotic maximum jaw growth increment at some initial size of sea urchin that sets the exponential term to zero; Δ_t is the actual time increment between tagging and recovery, i.e. ~1 year; L_t is the size when first tagged; L^m_{50} is the initial length at which the mid-way point between the $Max\Delta L$ and zero growth increment is reached; and L^m_{95} denotes the initial length at which 95% of the difference between zero and maximum increment is reached; $Ln(19)$ is a scaling parameter that defines the L^m_{95} point. The error term εL_t is additive and normal, and assumed to have a mean of zero and standard deviation σ_{Lt}, which is also defined as a function of predicted length. The standard deviation of the residual for each L_t was modelled as a power function of the expected growth increment with two parameters alpha and beta (Haddon et al. 2008):

$$\sigma_{Lt} = \alpha\left(\Delta\hat{L}_t\right)^{\beta} \qquad \text{(eqn. 2)}$$

Biometrics and morphometrics

To assess the morphological characteristics of *C. rodgersii* in macroalgal boundary and barrens habitats, 5 mass characters and 4 linear morphological dimensions were measured. It was necessary to track temporal patterns in some variables that varied seasonally, e.g. gonad weight. Mass characteristics for macroalgal boundary and widespread barrens habitats at St. Helens were sampled on 5 occasions over a ~12 month period (ca. 2.5 month interval) between March 2004 and April 2005. On each sampling occasion, 30 *C. rodgersii* in the size range of ~80-110 mm TD (to reduce potential size related biases in body indices, M. Byrne *pers. comm.*) were collected by divers from each site. All animals were dissected fresh and drained of coelomic fluid and any free-surface water, and component body parts were weighed individually, *viz.* gonads; test and spines; gut and gut contents; and lantern. Reproductive investment

was described by the gonad index (GI) calculated as the percentage of an individual's total body weight that was gonad. Gut index (GutI) was similarly calculated as the percentage of total body weight as gut plus gut contents. The relative abundance of different gut contents were scored by assessing the planar percentage cover of pellet types spread evenly across a dissecting dish (8 cm radius). Seasonally invariate mass characters, i.e. test weights (plus spines), and lantern weights, were pooled across sampling periods. An estimate of *C. rodgersii* biomass per m^2 of reef was obtained for each habitat type by multiplying the weight of the average sized sea urchin (drained of coleomic fluid) for each habitat by the density of sea urchins within each habitat.

Linear morphological dimensions of test diameter, test height, jaw length and longest spine length were measured with knife-edge callipers to nearest mm. Note that because the *C. rodgersii* spine canopy consistently forms an even hemisphere, the length of the longest spine provided a useful index of overall spine morphology, i.e. the next 50 longest spines were on average 82 % (± 0.6% SE) of the longest spine length, n= 28. Test thickness (at ambitus) was estimated using a micrometer (to 0.1 mm) clamped either side of a flat ambulacral plate.

Analyses

Growth curves between each habitat/ site combination were compared using likelihood ratio tests, *after* Haddon (2001). All other statistical analyses were undertaken using the SAS® software (v. 9.1). For ANOVA, data were checked for conformity to assumptions of homoscedasticity and normality. Where data were heteroscedastic, the transformation to stabilise variances was determined by the relationship between group standard deviations and means (Draper & Smith 1981). Transformations are expressed in terms of the untransformed variate, *Y*. Where appropriate, ANCOVA was undertaken by first testing for homogeneity of slopes among sites. If homogeneity of slopes was indicated, analysis proceeded to compare intercepts. Unless stated otherwise, the ANOVA/ ANCOVA model had 2 main factors of Habitat (fixed) and Site (random), and the mean square of Habitat*Site was used to test the significance of Habitat. Frequency distributions were compared between habitats and sites by a series of Kolmogorov-Smirnov tests with an appropriate level of protection against type I error for non-orthogonal tests by adjusting α using the Dunn-Sidak method.

Results

Growth

Annual growth of *Centrostephanus rodgersii* jaws was significantly faster in the macroalgal boundary habitat than in recently formed barrens habitat (Figure 2a&b). Size structure of *C. rodgersii* within macroalgal boundaries was bimodal and skewed towards larger individuals relative to adjacent barrens habitat, which consisted of a unimodal distribution dominated by intermediate sized individuals (Figure 3a). Jaw length frequency distributions showed broad similarity between habitats (Figure 3b) and conversion of jaw lengths to age (using habitat specific growth models) revealed broadly similar ages between barrens and macroalgal boundary habitats (Figure 3c).

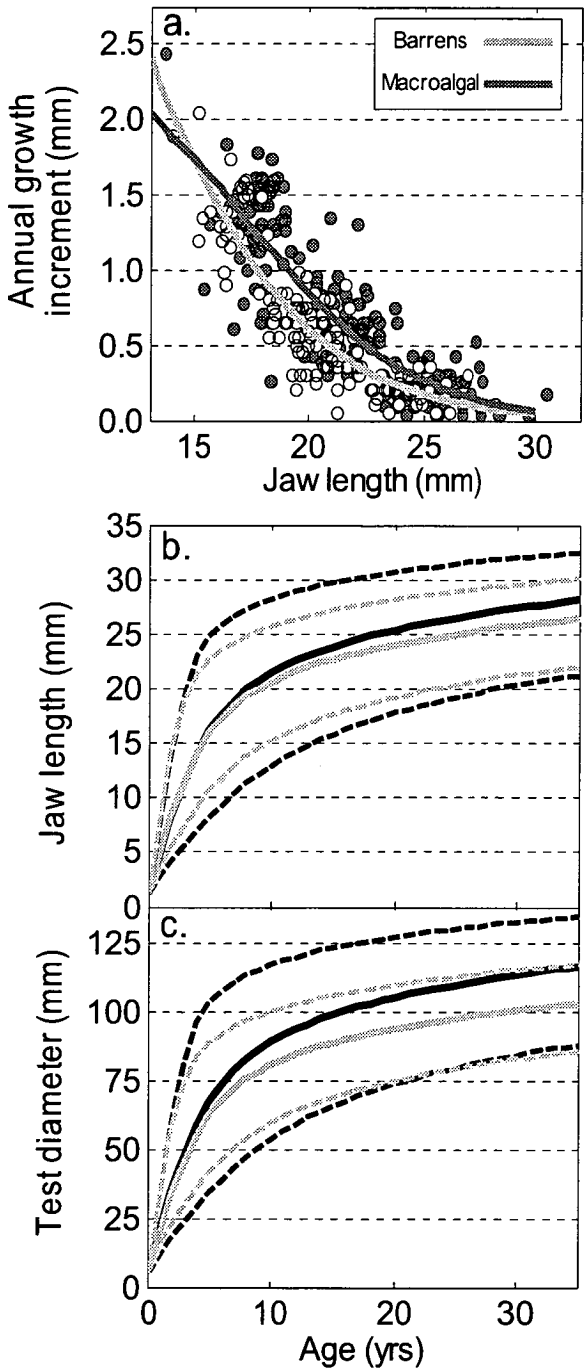

Figure 2. Growth of *Centrostephanus rodgersii* in recently formed barrens and macroalgal boundary habitat. (a) Growth of *C. rodgersii* jaws was best described by inverse logistic equations in both the macroalgal boundary habitat (filled circles) and barrens habitat (open circles). Likelihood-ratio tests revealed that growth models were significantly different between habitats ($P<0.0001$), but not among sites within habitats (macroalgal $P=0.67$; barrens $P=0.054$), thus growth for each habitat was modelled using data pooled within habitat type. Optimal inverse logistic parameters for macroalgal boundary: (eqn 1) $MaxΔL=2.622$, $L_{50}^{m}=17.369$, $L_{95}^{m}=27.663$, (eqn 2), $\alpha=0.284$, $\beta=0.451$; barrens (eqn 1), $MaxΔL=5.448$, $L_{50}^{m}=12.104$, $L_{95}^{m}=23.259$, (eqn 2) $\alpha=0.265$, $\beta=0.490$). (b) Growth curves by Test Diameter obtained using habitat specific conversion between TD and jaw length; macroalgal, TD= $4.14*jawL$, $R^2=0.66$; barrens TD=$3.90*jawL$, $R^2=0.78$). Broken lines indicate respective 95% confidence intervals obtained by bootstrap re-sampling 1000 times. Note that due to a lack of data for small size classes (<13 mm law length), juvenile growth was standardised across habitats using the optimal $MaxΔL$ for all data pooled across habitats.

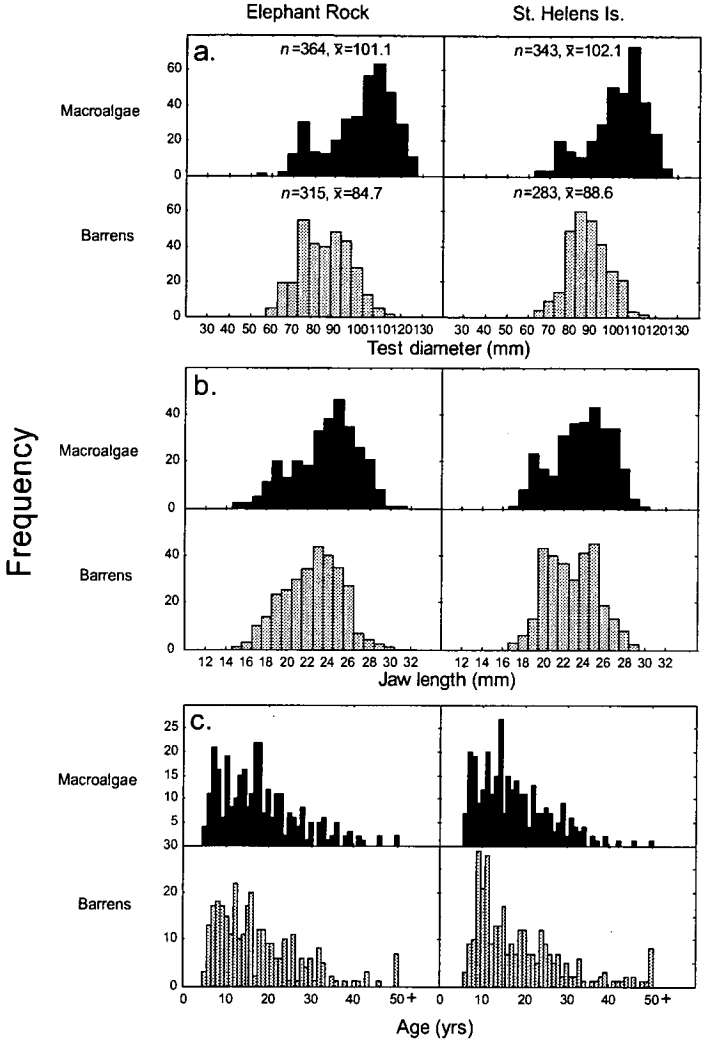

Figure 3. Test diameter, jaw length and age frequencies of *Centrostephanus rodgersii* on recently formed barrens and adjacent macroalgal boundary habitat. a) Test diameter frequency at time of tagging in 2004; all pair-wise Kolmogorov-Smirnov comparisons yielded significant differences, except for comparison of urchins from macroalgal habitat at the two sites P=0.68 (Dunn-Sidak adjusted α=0.0085). (b) Jaw length frequency in 2005, n=300; and (c) age frequency estimated from jaw lengths using the appropriate habitat-specific growth function (Figure 2b) adjusted for age as at 11/10/2005, n=300. Comparison of age frequencies revealed non-significant differences in age distributions between all samples (KS tests minimum P=0.12).

Biometrics

Temporal patterns in *C. rodgersii* body indices show that gonad indices (GIs) were generally higher within the macroalgal boundary relative to the barrens, however this difference was not significant during the peak of the spawning period (Figure 4a; Model III 2-way ANOVA; 'Habitat', $F_{(1,1)}$=76.87, P=0.072, 'Site', $F_{(1,116)}$, P=0.200,

'Habitat*Site', $F_{(1,116)}$, P=0.704). Gut indices were generally higher for *C. rodgersii* in the macroalgal boundary habitat year around, and comparison of elevated gut indices during the post spawning period revealed a significant habitat effect (Figure 4b; Model III 2-way ANOVA; 'Habitat', $F_{(1,1)}$=191.23, P=0.046, 'Site', $F_{(1,116)}$=32.04 P=<0.0001, 'Habitat*Site', $F_{(1,116)}$=0.53, P=0.467). Gut contents of *C. rodgersii* at macroalgal boundaries consistently contained greater proportions of fleshy macroalgal material relative to urchins from barrens habitat that predominantly contained filamentous and encrusting algal material (Figure 4c; Model III 2-way ANOVA for post spawning period revealed a significant interaction: $Y^{0.68}$, $F_{(1,116)}$=7.38, P=0.008). The biomass of *C. rodgersii* occurring within the macroalgal boundary (546.86 ± 91.46 SE gm^{-2}) was not significantly different to that in adjacent barrens habitat (453.62 ± 166.28 SE gm^{-2}) (1-way ANOVA, $F_{(1,2)}$=0.24, P=0.67).

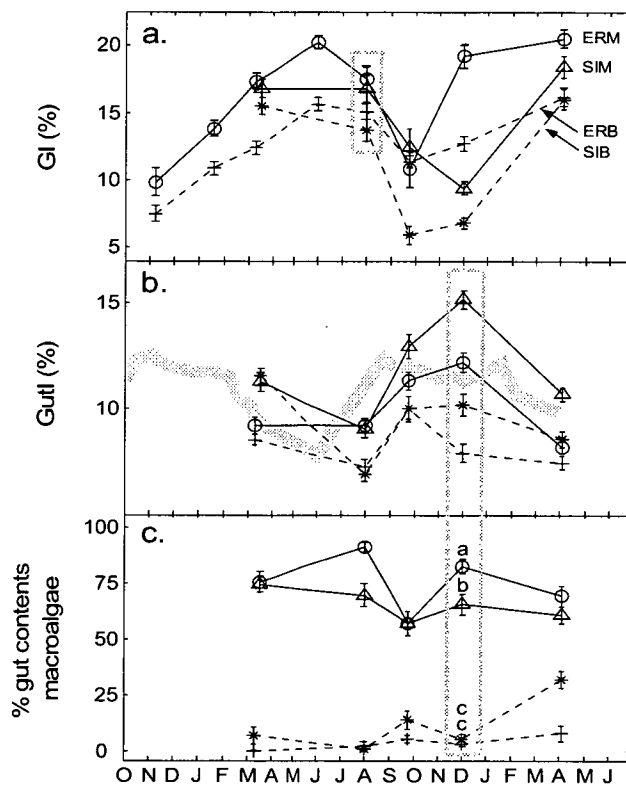

Figure 4. Temporal pattern of *Centrostephanus rodgersii* body indices within recently formed barrens and macroalgal boundary habitat, 2004 to 2005. Data are means ±SE (n=30). Solid lines = macroalgal boundary [Elephant Rock Macroalgal (ERM)=O; St. Helens Is Macroalgae (SIM)=Δ]; broken lines = barrens [Elephant Rock Barren (ERB) =+; St. Helens Is. Barren (SIB)=*]. (a) Gonad indices, pre-spawning peak shown by dash-dot box. (b) Gut indices, grey background band represents gut index cycle obtained across 3 additional sites in eastern Tasmania (*refer to* Ling et al. 2008). (c) Gut contents, habitat by site REGWQ groupings for the post-spawning period (dash-dot box) are indicated by different letters, α = 0.05.

Morphometrics

On average, *C. rodgersii* from the recently formed barrens possessed longer jaws for a given test diameter compared to urchins from the macroalgal boundary habitat (Figure 5a; revealed different slopes across habitats ($F_{calc(3,1192)}$=3.26, P<0.001); while slopes were homogenous within each habitat type (Barrens, $F_{1,596}$=1.88, P=0.17; Macroalgal boundary, $F_{1,596}$= 0.00, P=0.96). Conversely, total body weight of *C. rodgersii* (including spines) was significantly heavier on average within the macroalgal boundary habitat relative to animals of similar test diameter on the barrens. However, there was also significant variability in relative body weight among sites and among habitats across sites (Model II, 2-way ANCOVA, test for homogeneity of slopes, $F_{calc(3,592)}$=0.89, P>0.25; 'Habitat', $F_{(1,1)}$=115.07, P<0.0001; 'Site', $F_{(1,1)}$=31.09, P<0.0001; 'Habitat*Site', $F_{(1,595)}$=9.43, P=0.002).). Heavier body weight, corrected for test diameter, within the macroalgal boundary habitat was explained by these urchins having relatively thicker tests than their counter parts on barrens habitat (Figure 5b; 1-way ANCOVA, test for homogeneity of slopes, $F_{(1,84)}$=0.01, P=0.94; 'Habitat', $F_{(1,85)}$=21.69, P<0.0001).

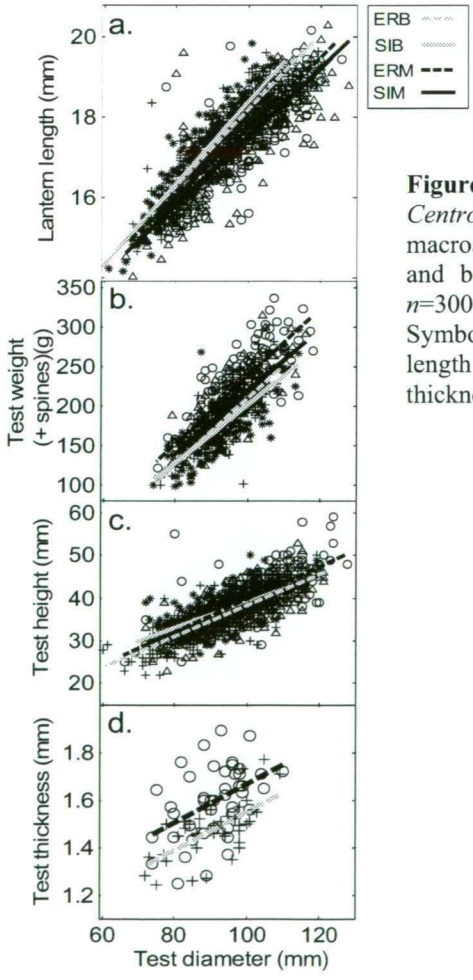

Figure 5. Jaw and test characteristics of *Centrostephanus rodgersii* within macroalgal boundary (black trendlines) and barrens habitats (grey trendlines), n=300 except for (d) where n=44. Symbols as for figure 4. (a) Lantern length *vs.* test diameter; (b) Test thickness *vs.* test diameter.

Spine length relative to test diameter was generally longer for sea urchins from the open barrens habitat than those within the macroalgal boundary zone. Across habitats, spine length for *C. rodgersii* generally increased with increasing test diameter to about 70 mm, and thereafter a slight increase in spine length was observed for urchins from barrens, but for individuals from macroalgal habitat, the spine length declined with increase in test diameter, indicating net spine erosion through time (Figure 6a). For St. Helens data (>75 mm TD), comparison of longest spine *vs.* test diameter yielded significantly different slopes between samples (test for homogeneity of slopes, $F_{calc(3,1192)}$=4.75, P<0.001), however slopes were not detectably different within habitat type (Barrens, $F_{1,596}$=0.36, P=0.55; Macroalgal; $F_{1,596}$=0.30, P=0.58).

Consistent with the pattern of spine erosion observed at macroalgal boundaries at St. Helens, *C. rodgersii* from incipient barrens further to the south in eastern Tasmania displayed a similar negative relationship between spine length and test diameter (Figure 6b; slopes of spine length *vs.* test diameter for urchins from incipient barrens and macroalgal boundary samples were all negative and not statistically different from each other ($F_{3,1578}$=0.86, P=0.46); conversely, for widespread barrens, spine length was positively related to test diameter and this slope was statistically different to the negative slopes described for urchins from incipient barrens $F_{3,1578}$=8.67, P<0.0001). Differences in spine morphology between *C. rodgersii* on open barrens habitat and those only a few metres distant in the macroalgal habitat are visually obvious (Figure 7).

Discussion

Growth, diet and morphology

Similar age-structure of *Centrostephanus rodgersii* existing amongst macroalgae and recently formed barrens suggests that both habitats are influenced by broadly similar recruitment events and that there is no pronounced ontogenetic shift in habitat preferences. Importantly, the emergence of distinctive growth and phenotypic patterns between the alternative reef states indicates persistence of *C. rodgersii* within each habitat and limited exchange of individuals across this habitat interface (e.g. Konar 2000). Consistent with that observed for *C. rodgersii* within its historical NSW range (Blount 2004), and with sea urchins in other systems (e.g. Rowley 1990; Meidel & Schiebling 1999), *C. rodgersii* grew significantly faster within macroalgal habitat of the extended eastern Tasmanian range. Furthermore, faster growth of *C. rodgersii* within macroalgal habitat was consistent with relatively heavy gut weights and a diet composed predominantly of fleshy macroalgae. In adjacent barrens the smaller, slower growing sea urchins displayed lower gut weights for a given size and a diet of predominantly filamentous and encrusting coralline algae with fleshy macroalgae consumed only occasionally (e.g. Harrold & Reed 1985). The persistence of sea urchins on reefs where algae has been heavily grazed is clearly dependent on the ability of sea urchins to switch diet from fleshy macroalgae to filamentous/ coralline algae (*reviewed by* Johnson & Mann 1982). However, in contrast to many other studies (e.g. Lang & Mann 1976; Johnson & Mann 1982; Meidel & Schiebling 1998), including the pattern demonstrated by *C. rodgersii* in NSW (Byrne et al. 1998), habitat-related patterns in nutritional status were not reflected as strong contrasts in gonad index. This

intriguing result indicates that individuals on recently formed barrens in eastern Tasmania obtain sufficient nourishment to invest strongly in reproduction, but appear to do so at the expense of somatic growth. Because population densities of *C. rodgersii* on Tasmanian barrens (1-2 m^{-2}) are ~2-4 times lower than in NSW (Johnson et al. 2005), reduced competition between individuals for food may explain the greater than expected gonad indices on recently formed Tasmanian barrens (e.g. Wahle & Peckham 1999).

Intriguingly, the biomass density of *C. rodgersii* (g m^{-2}) was not significantly different between macroalgal and barrens habitats however the sea urchin was more numerous per unit biomass on the barrens. Such a pattern is typically observed across the historical NSW range where *C. rodgersii* densities on barrens are approximately twice that found within fringing macroalgal habitat (Underwood et al. 1991; Blount 2004; *also see* Andrew & Byrne 2001). As inferred from observations within the sea urchins historical range (Andrew 1991; Blount 2004), lower densities of *C. rodgersii* within macroalgal habitat but similar age-structure to that observed on adjacent barrens, suggests relatively greater rates of sea urchin settlement to grazed habitats. However, because we were unable to effectively sample recently settled *C. rodgersii* (due to the cryptic nature of such small individuals), it remains unclear whether differential settlement of the sea urchin occurs across the contrasting habitat types. Alternatively, it is possible that recruitment of individuals into the macroalgal habitat may occur largely via the post-settlement accumulation of individuals at algal interfaces due to the relatively greater movement rates of sea urchins on barrens compared to that observed in macroalgal habitat (e.g. Mattison et al. 1977; Lauzon-Guay & Scheibling 2007).

Consistent with contrasting growth rates of *C. rodgersii* across the alternative habitat states, comparisons of relative jaw length and test thickness (both of which are indicators of food-limitation in sea urchins; Ebert 1980; Black et al. 1982; 1984), also revealed clear differences between habitats. Consistent with observations from within the sea urchins historical range (Andrew & Byrne 2001; Blount 2004), *C. rodgersii* from the recently formed Tasmanian barrens possessed longer jaws, but thinner tests, for a given test diameter relative to sea urchins in the macroalgal boundary habitat. Individuals from macroalgal habitat also had shorter spines for a given test diameter than their counterparts on adjacent barrens, reflecting that they are subject to abrasion and breakage by the sweeping action of robust macroalgae (S. Ling *pers. obs.*). Thus, broadly distinctive phenotypes of *C. rodgersii* emerged from within the extension-region; sea urchins with a large and thick test but relatively small lantern and short spines were observed to forage among macroalgae; while sea urchins from the barrens habitat possessed relatively small and thin tests, but large jaws and longer spines.

Informing macroalgal-urchin dynamics within the newly extended range

While juvenile plants and foliose understorey species are highly susceptible to sea urchin grazing, under some circumstances large adult plants, particularly canopy forming macroalgae such as *P. comosa* and *E. radiata* (found in both NSW and eastern Tasmania) appear to have a partial size refuge from *C. rodgersii* (Andrew & Byrne 2001; Hill et al. 2003). Under the influence of ocean surge typical of the exposed Tasmanian coastline, large plants appear particularly immune to sea urchin grazing by

restricting the distribution of urchins with robust, yet flexible lamina that create a whiplash effect on the benthos (e.g. Himmelman 1980; Vasquez & McPeak 1998; Konar 2000; Gagnon et al. 2003).Thus, invasion of mature Tasmanian macroalgal beds and persistence of *C. rodgersii* within this habitat may become difficult under conditions of surge. Indeed, the domination of shallow exposed Tasmanian reefs by dense mature stands of macroalgae (i.e. *P. comosa* which is commonly found to depths

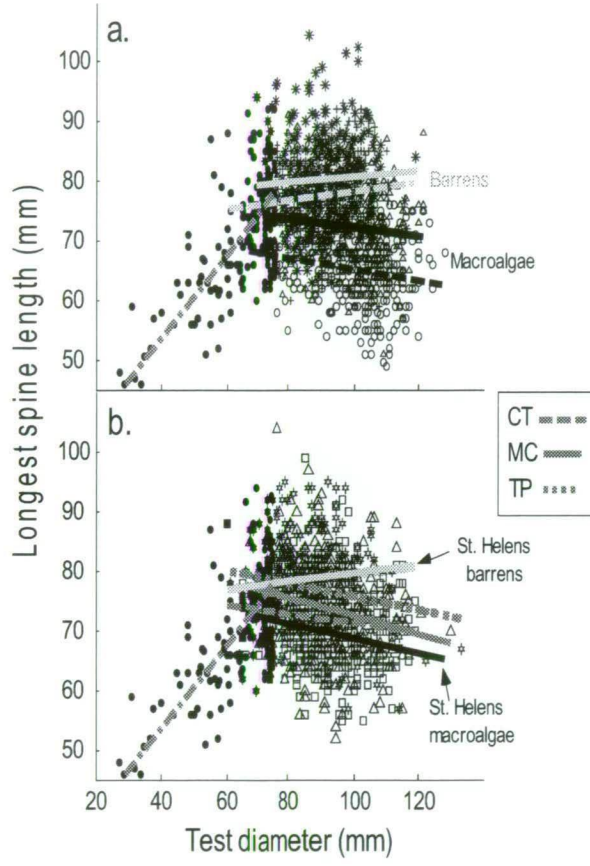

Figure 6. Spine length versus test diameter for *Centrostephanus rodgersii* in recently formed barrens and macroalgal habitat. (a) Macroalgal boundary and barrens habitats at St. Helens, symbols and trend lines as for previous figures except for small dots representing additional data for smaller size classes of *C. rodgersii* (<75 mm) obtained across eastern Tasmania and the dash-dot trendline fitted to these data (b) Longest spine *vs.* test diameter for sea urchins from incipient barrens relative to trends at St. Helens; symbols are Cape Tourville (CT)=squares, n=345; Mistaken Cape (MC)=triangles, n=353; Tasman Peninsula (TP)=stars, n=288; refer to legend for trendlines. Note that in (b) trendlines for St. Helens are based on data pooled within each habitat type (n=600), but data points for these samples not shown.

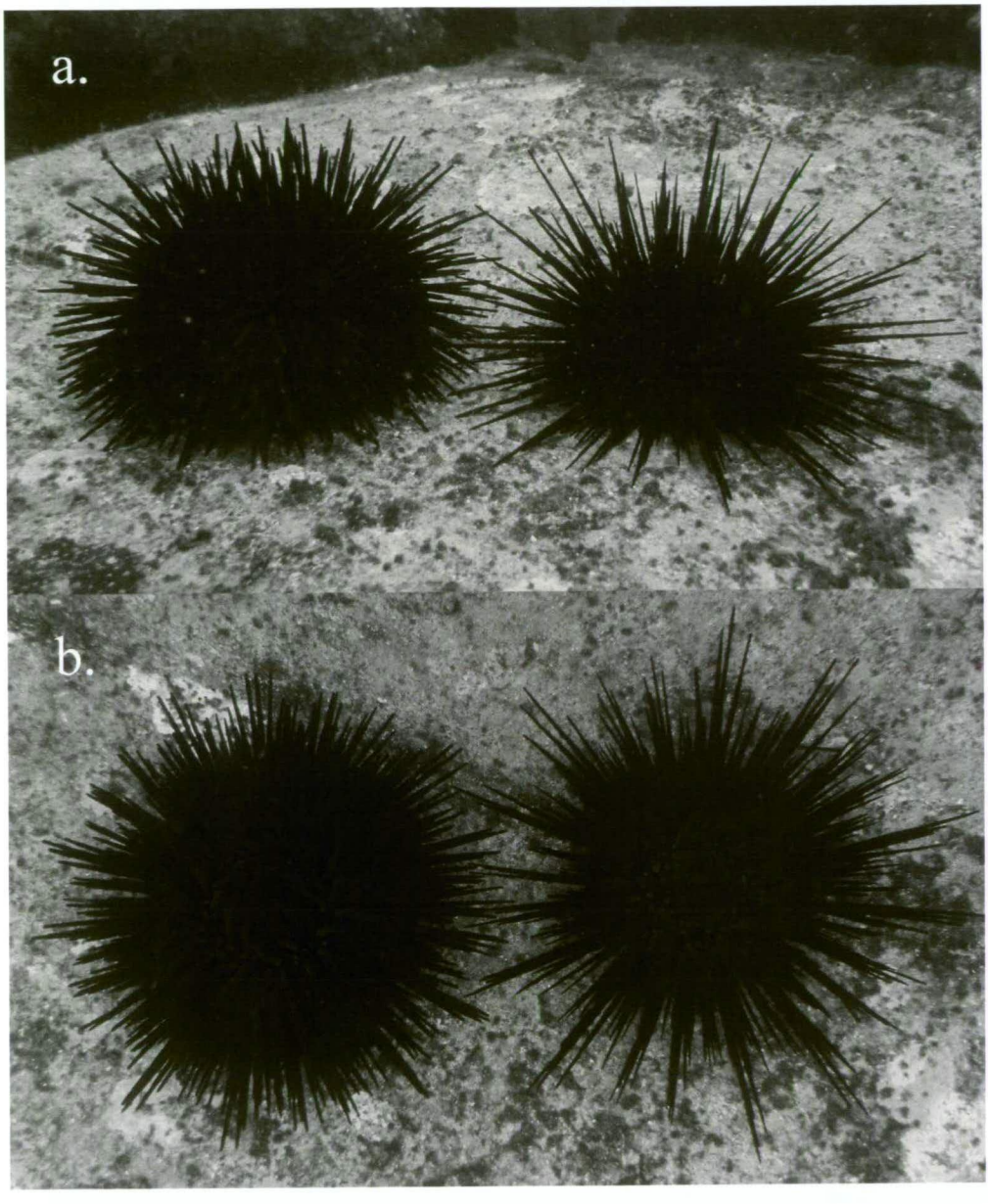

Figure 7. Typical *Centrostephanus rodgersii* specimens from macroalgal boundary habitat (LHS) (TD=110 mm) and recently formed barrens (RHS) (TD=82 mm). (a) Oblique view; (b) Aboral view. Individuals were collected from adjacent habitat states at a depth of 10 m; Note that although the TD is 28 mm smaller for the barrens specimen, the diameter of the spine canopy is greater than that of the larger individual from within the macroalgal boundary habitat. Estimated age for the displayed individual from the macroalgal boundary habitat is ~30 y, while the individual from the barrens is ~12 y.

of ~10 m) emerges as a likely factor influencing the currently deep (> 10 m) depth distribution of *C. rodgersii* on this coast (Johnson et al. 2005).

The presence of adult macroalgae also appeared to influence the morphology of *C. rodgersii* as the short-spined configuration was particularly striking where individuals were bound to crevices within the range of whiplash from macroalgal fronds (*see* Figure 7). Indeed, in other work we observed that long-spined *C. rodgersii* from barrens habitat, when held in cages with large macroalgal plants, all displayed short spines after ~6 months. Conversely, short-spined individuals from macroalgal habitat began to re-grow length in their spines (observed as pale growing tips) when held in aquaria free of macroalgae abrasion for several months (also observed for *Strongylocentrotus franciscanus* by Rodgers-Bennett et al. 1995). Furthermore, short-spined *C. rodgersii* also possessed thicker and heavier tests. Consistent with this pattern, breakage of spines in *S. purpuratus* results in greater overall rates of calcification resulting in thicker, heavier and more robust tests (at the expense of re-growth in spine length) arguably better suited to exposed coastal conditions (Edwards & Ebert 1991). Thus plastic resource allocation of sea urchins would appear capable of shifting to favour persistence within exposed macroalgal dominated habitats.

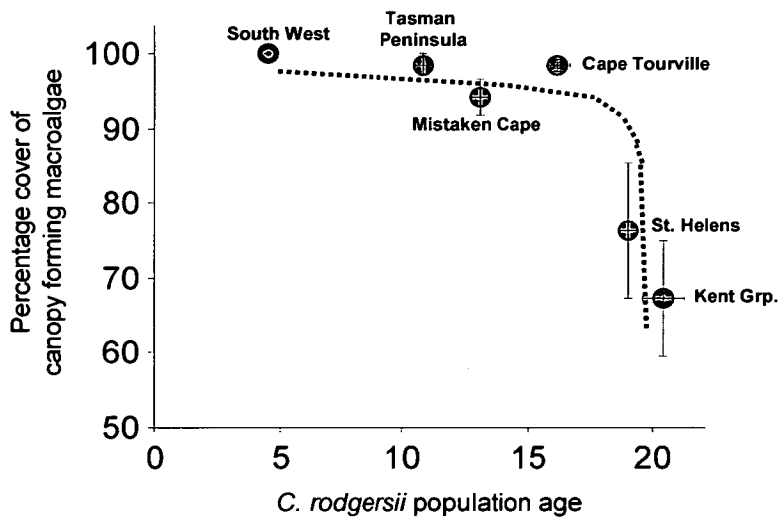

Figure 8. Cover of canopy forming macroalgae versus mean population age of *Centrostephanus rodgersii* on rocky reefs across the range-extension region, data are means ±SE. Macroalgal data for eastern Tasmania is for reefs 5-18 m depth from Johnson et al. 2005; for South West Tasmania only 3 *C. rodgersii* individuals and no barrens have been reported, hence the luxuriant macroalgal cover observed across this region was considered to constitute 100%. Mean age was estimated for each location from the jaw lengths of 300 individuals, except for the Kent Group and South West Tasmania where age was estimated from test diameters, n=273 and n=3 respectively. Dotted-line was fitted by eye indicating a threshold type relationship.

Importantly, the final transition from macroalgal beds to *C. rodgersii* barrens appears to occur when large mature plants, often weakened by grazing of haptera (S. Ling *pers. obs.*), either break away during surge or senesce (e.g. Harrold & Reed 1985; Tegner et al. 1995). Thus, providing *C. rodgersii* can persist within swell prone macroalgal habitat, eventual felling of large robust plants may allow barrens habitat to expand into shallower reef margins (< 10 m depth) as commonly observed within the species historical range (e.g. Andrew 1993; Andrew & Byrne 2001). Indeed, overgrazing by *C. rodgersii* within the extension-region is associated with relatively mature sea urchin populations as widespread barrens are only currently observed at sites where the average population age is > 18 years (Figure 8). Such a pattern suggests a time delay between the incursion of the sea urchin and the onset of barrens formation, indicating that if populations are able to grow then patterns of grazing within the extension-region may converge on that observed within the species historical range.

Barrens formation and range expansion

In creating a habitat free of large and potentially 'inhibitory' macroalgae, formation of barrens by *C. rodgersii*, while resulting in reduced individual performance through lower food availability, may manifest as a net positive feedback at the population level (e.g. Jones et al. 1997; Scheffer et al. 2001). That is, *C. rodgersii* may be considered to facilitate its own invasion success in eastern Tasmania by modifying the macroalgal habitat and effectively 'paving the way' for further establishment of high density sea urchin populations (*also see* Breen & Mann 1976; Lang & Mann 1976; Himmelman 1980; Tegner 1980; Tegner & Dayton 1981; Miller et al. 2007). Indeed, Mann and Breen (1972) first hypothesised that observations of increased sea urchin abundance associated with barrens may indicate that the creation of barrens habitat facilitates urchin population expansion. Since then, this possibility has received little focus (*but see* Lang & Mann 1976). Rather, emphasis has been placed on the negative effects of barrens at the individual level, even though the formation of barrens habitat has been documented to enhance localised carrying capacity (Lang & Mann 1976; Himmelman 1980), post-settlement survival (Rowley 1989), population stability and recruitment (e.g. Andrew & Byrne 2001), and enhance population level reproductive success by spatially aggregating free-spawning sea urchins (e.g. Wahle & Peckham 1999).

Because a greater number of individuals may exist on barrens for a given biomass of sea urchins, overgrazing of large and abrasive macroalgal plants on swell prone reefs appears to be a mechanism by which sea urchins may establish highly abundant populations. In the case of a range-extending sea urchin occurring at relatively low population size at a range margin (where risk of local extinction may be high), the conversion of macroalgal dominated reef to sea urchin barrens therefore appears to be an important invasion process facilitating the establishment of viable populations. Furthermore, population stability of sea urchins may also be increased by minimising individual predation risk. Because long spines appear to confer greater resistance against sea urchin predators, predation risk to *C. rodgersii* is seemingly lower on barrens where individuals can afford relatively long spines. Based on habitat specific growth models (Figure 2c) and measures of size-specific lobster predation (*see* Chapters 6 & 7), the short-spined morph of *C. rodgersii* occurring in macroalgal habitat takes approximately 21 years on average to reach a size refuge from all but the very largest lobsters. In contrast, the long-spined morph of *C. rodgersii* characteristic

of the barrens habitat, even though it has slower growth in test diameter, develops a spine canopy allowing predatory size refuge much quicker at approximately 15 years.

Conclusions

Within the extension-region, habitat-specific patterns of *C. rodgersii* were broadly consistent with that observed from within the historic range. This suggests that the dominant ecological role and ecological dynamics of the species will be conserved across its extended range. A notable contrast however, was the exceptional reproductive status of sea urchins within recently formed barrens. Nonetheless, because individual gonad production is known to vary in a density-dependent manner among sea urchins (e.g. Andrew 1989; Byrne et al. 1998; Blount 2004), this result suggests that if population size were to increase within the extension-region then habitat-specific contrasts in reproductive condition would converge on that observed within the species historical range. Indeed, further coastal warming predicted for the extension-region (*reviewed by* Poloczanska et al. 2007) appears set to facilitate further population expansion of *C. rodgersii* (Ling et al. 2008; *see* Chapters 2&3), thus the ecological importance of the sea urchin in this system is likely to increase. Finally, because of the typically low functional-diversity observed across temperate rocky reef ecosystems (e.g. Steneck et al. 2002; Micheli & Halpern 2005), our results indicate that the climate-driven addition of functionally important species to higher latitudes can result in major change to the dynamics of temperate marine systems.

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CHAPTER 6: FISHING REDUCES RESILIENCE OF KELP BEDS AGAINST A RANGE EXTENDING BARRENS-FORMING SEA URCHIN

Abstract

Recent catastrophic shift from productive kelp beds to sea urchin barrens on rocky reefs in eastern Tasmania (Australia) has been caused by the range expanding sea urchin *Centrostephanus rodgersii* (Diadematidae). Given climate change projections and population trends of this sea urchin since its first detection in Tasmania only ~30 years ago, there is strong likelihood of further increases in population size and widespread barrens formation. Coincident with the arrival of *C. rodgersii* is heavy fishing of rocky reef systems in Tasmania. We used multiple experiments to examine the possibility that a reduction in effective predator biomass has reduced resilience of kelp beds and increased the likelihood of widespread barrens formation by *C. rodgersii*. Remote video surveillance inside no-take Marine Protected Areas (MPAs) identified that the spiny lobster, *Jasus edwardsii* (Palinuridae), frequently predated tethered and non-tethered *C. rodgersii* and was a more important predator of *C. rodgersii* than fish. Predation rates on tethered *C. rodgersii* were much higher inside a no-take MPA (high lobster abundance) compared to an adjacent fished reef (low lobster abundance). Notably, there was no difference between protected and unprotected reef in the abundance of predatory fishes that could potentially prey on the sea urchin. In a tagging experiment, we tracked the fate of *C. rodgersii* inside and outside two MPAs and revealed that apparent daily survivorship was reduced and cryptic behaviour (affecting resighting probability) increased inside MPAs relative to fished sites. Finally, estimates of lobster size from video footage of predation, together with *in situ* caging and laboratory experiments, revealed that only supra-legal sized lobsters (carapace length ~> 140 mm) were capable of effectively preying on *C. rodgersii*. Because of intensive fishing, these large lobsters are now functionally extinct along much of the coastline. Our combined evidence suggests strongly that removal of large (supra-legal) predatory-capable lobsters has effectively reduced resilience of macroalgal beds and increased the risk of wide-spread barrens formation by the range extending *C. rodgersii*. It is likely that management aimed at increasing the abundance of large predatory lobsters will increase kelp bed resilience and reduce the risk of further catastrophic events in the face of ongoing climate warming. These findings have important implications for conceptual models of temperate rocky reef communities.

Introduction

Globally, the structure and function of ecosystems are becoming increasingly challenged by human activities. Ecosystems appear resilient to some levels of perturbation but catastrophic shifts in structure and function can occur, with a return to former states unlikely, once a critical threshold is passed (e.g. May 1977; *reviewed by* Scheffer et al. 2001; Scheffer & Carpenter 2003). Identifying how human activities affect ecosystem resilience (*after* Holling 1973) is imperative to managing the risk of entering trajectories of catastrophic change and loss of important ecosystem services (e.g. Steneck et al. 2002;; Bellwood et al. 2004; Folke et al. 2004; Hughes et al. 2005).

In marine ecosystems, fishing is a major perturbation and driver of change (e.g. Pauly et al. 1998; Jackson et al. 2001). Effects of fishing are readily observed locally (e.g. Dayton et al. 1998; Edgar & Barrett 1999; Shears & Babcock 2002) and serial depletion by industrialised fishing fleets has led to global impacts across the world's oceans (Myers & Worm 2003; Pauly et al. 2005; Berkes et al. 2006). While fishing has clear effects on the mortality rates of harvested populations, fishing may also lead to catastrophic ecosystem shifts as a result of habitat destruction and altered trophic organisation (*reviewed by* Pauly et al. 1998; Pinnegar et al. 2000; Tegner & Dayton 2000; Jackson et al. 2001; Myers & Worm 2003; Steneck et al. 2002, 2004; Scheffer et al. 2005; Berkes et al. 2006; Worm et al. 2006).

Climate change is another major perturbation that is impacting marine ecosystems globally (*reviewed by* Harley et al. 2006). Given the range of current climate change projections (*reviewed by* Meehl et al. 2007), impacts on marine ecosystems are likely to be profound. While overfishing and global climate change may independently pose major threats to ecosystem dynamics, synergism between such large scale perturbations may lead to unprecedented risk of catastrophic shifts in coastal ecosystems (e.g. Dayton et al. 1998; Jackson et al. 2001; Hughes et al. 2003; Bellwood et al. 2004; Scheffer et al. 2005; Harley et al. 2006).

One of the most widely documented catastrophic shifts in temperate coastal marine ecosystems is the transition from productive seaweed beds to 'barrens' habitat as a result of overgrazing by sea urchins (*reviewed by* Lawrence 1975; Chapman & Johnson 1990; Pinnegar et al. 2000; Steneck et al. 2002). Driven by a changing climate, the long-spined sea urchin, *Centrostephanus rodgersii* (Agassiz) has recently invaded eastern Tasmania and initiated catastrophic ecosystem shift by overgrazing macroalgae and maintaining an alternative stable state of barren, unproductive habitat (Johnson et al. 2005; Ling 2008; Chapters 4 & 5). Consistent with the fingerprint of climate change (Parmesan & Yohe 2003), long-term change to the East Australian Current (EAC) (*see* Ridgway 2007) has resulted in the poleward (southward) range extension of many marine species, including *C. rodgersii*, in this region (*reviewed by* Poloczanska et al. 2007). Possessing a long-lived pelagic larval stage (~100 days, Huggett 2005), *C. rodgersii* has the potential for extended oceanic dispersal, and the spatial distribution and age structure of *C. rodgersii* in eastern Tasmania is correlated with the proximity to the EAC (*see* Chapter 3). Furthermore, warming trends on the east coast of Tasmania (Ridgway 2007) coincide with the timing of arrival of the sea

urchin, and given projections of ongoing warming, the Tasmanian coast is becoming increasingly favourable for *C. rodgersii* to complete its life cycle (Ling et al. 2008, Chapter 2).

In temperate Australia, no other benthic herbivore has as large an effect on shallow reef communities as *C. rodgersii* (Fletcher 1987; Andrew 1991; Andrew & Underwood 1992; Ling 2008). In central and southern New South Wales (NSW) this species maintains barrens habitat over ~50% of shallow reef (Andrew & O'Neill 2000). The destructive grazing of seaweeds and benthic invertebrates has strong negative flow-on effects to local biodiversity (Ling 2008; Chapter 4) and lucrative reef-based fisheries (Shepherd 1973; Andrew & Underwood 1992; Andrew et al. 1998; Worthington et al. 1998; Johnson et al. 2005). Importantly, the 'catastrophic shift' (*after* Scheffer et al. 2001) from small grazed patches (<1-10s m) to widespread sea urchin barrens (100s m) occurs when localized grazed patches coalesce (Andrew 1993; Andrew & Underwood 1993; Hill et al. 2003). Typical of other members of the Diadematid family, *C. rodgersii* is highly nocturnal and displays a homing behavior whereby localized grazing is predominantly manifest as grazed halos radiating from crevices used for daytime shelter (Andrew 1988; Jones & Andrew 1990; Underwood et al. 1991). From studies in NSW, it is clear that there is a critical density of *C. rodgersii* required to initiate widespread destructive grazing of macroalgae with return to the macroalgal state rarely observed once this threshold density is reached (Andrew 1989; Andrew 1991; Andrew & Underwood 1993; Hill et al. 2003).

Given the drastic change in structure and functioning associated with the shift from seaweed-dominated to barrens states (e.g. Chapman 1981; Duggins et al. 1989; Babcock et al. 1999), attempts to identify the mechanism(s) underpinning this transition has long engaged marine ecologists. While mechanisms and dynamics of barrens formation are complex and often peculiar to particular systems, the most prevalent explanation is that over-harvesting of sea urchin predators results in predatory release and subsequent formation of sea urchin barrens, i.e. conforming to the paradigm of 'top-down' control (*reviewed by* Steneck 1998; Pinnegar et al. 2000; Tegner & Dayton 2000; Steneck et al. 2002; Halpern et al. 2006). While several species have been identified to consume *C. rodgersii* in NSW, including the labrid *Achoerodus viridis* (Gillanders 1995) and the heterodontid shark *Heterodontus portusjacksoni* (McLaughlin & Gower 1971), the impact of these predators on sea urchin populations and effects of fishing on these predators is unknown (*reviewed by* Andrew & Byrne 2001).

Superimposed on the climate driven arrival of *C. rodgersii* in eastern Tasmania is heavy exploitation of rocky reef ecosystems (e.g. Frusher 1997). Long-term changes to reef ecosystems in Marine Protected Areas (MPAs) relative to adjacent fished sites in eastern Tasmania show that fishing has a major impact on the abundance and size structure of harvested species (Edgar & Barrett 1999), including potential predators of *C. rodgersii*. Given the climate-driven advance of *C. rodgersii* in eastern Tasmania and strong likelihood of further increases in population size and extent of barrens (Johnson et al. 2005; Ling et al. 2008; *see* Chapters 2 & 3), there is an urgent need to understand how biological interactions may influence the likelihood of catastrophic shift from diverse macroalgal beds to the impoverished barrens state. Given that

fishing down sea urchin predators has been implicated as a key process of barrens formation worldwide (*op cit*), this study addresses the hypothesis that fishing has reduced sea urchin predators and therefore reduced resilience of kelp bed ecosystems against catastrophic overgrazing by a range-extending sea urchin. Indeed, such an approach does not constitute a traditional test of equilibrium-based paradigms whereby systems are considered to be structured by either 'top-down' or 'bottom-up' effects. Rather this approach encompasses multiple processes acting simultaneously at large spatial and temporal scales, and incorporates the concept of nonequilibrial dynamics in determining the likelihood of ecosystem change (*after* Hughes et al. 2005; Scheffer et al. 2005).

To examine the effect of predators on *C. rodgersii* in Tasmania, we first attempted to identify predators. Any impact of fishing on these predators, and ultimately on *C. rodgersii*, was then examined by comparing survival of *C. rodgersii* on reefs inside MPAs (high predator biomass) relative to fished reefs (low predator biomass). Finally, the size-specific nature of predation interactions was examined in context of size-selective fishing pressure within the sea urchin's extended range.

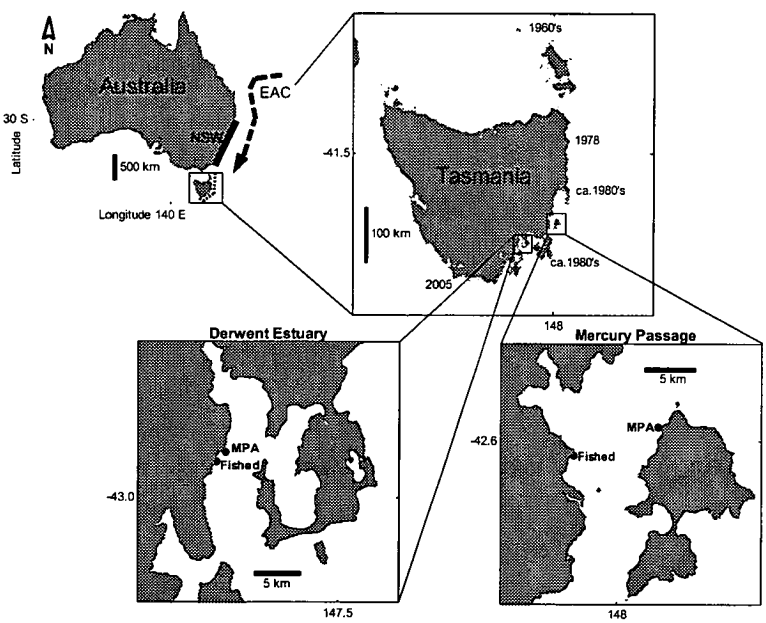

Figure 1. Map of Tasmania showing locations and sites where predation experiments were undertaken. Accompanying the map of Australia is the directional influence of the East Australian Current (EAC); the 'native' distribution of *C. rodgersii* on the Australian mainland (solid line, after Andrew & Byrne 2001); and the recent range expansion of the sea urchin (dotted line, after Johnson et al. 2005). Expanded Tasmanian map shows the timing of first sightings of *C. rodgersii* along this coastline (after Johnson et al. 2005; J. Valentine *pers. obs.*). Expanded Derwent Estuary and Mercury Passage regions display MPAs (CPMR and MIMR respectively) and nearby Fished reefs (Alum Cliffs and Johnson's Point respectively).

Materials and Methods

Study sites

Experiments were performed in two eastern Tasmanian regions where predator biomass has shown strong recovery inside MPAs relative to adjacent reefs subject to exploitation (Edgar & Barrett 1999; Edgar & Barrett *unpub. data*). The Maria Island Marine Reserve (MIMR, Mercury Passage) was established in 1992 and had therefore experienced 12 yrs of protection from fishing at time of experimentation in 2004; the Crayfish Point Marine Reserve (CPMR, Derwent Estuary) was established in 1971 and had thus experienced 33 yrs protection at time of experimentation (*see* Figure 1). Experimental reefs were of high relief, experienced moderate wave exposure, and supported seaweed communities. Given low abundances of *C. rodgersii* within the immediate vicinity of the experimental reefs, animals were collected at other sites and transferred to experimental reefs to simulate invasion of reefs by the sea urchin.

Identifying predators: Remote video monitoring of *Centrostephanus rodgersii* inside MPAs

Given the strong nocturnal behaviour of *C. rodgersii*, a remotely operated continuously recording video system equipped with infrared lighting was used to enable detection of predatory interactions throughout the diel cycle while eliminating potential effects of visible light on animal behaviour (for details *see* Mills et al. 2005). To maximise the ability to detect naturally occurring predators, the video system was set-up inside MPAs. Because of relatively high nocturnal movement in *C. rodgersii* and limited camera view-field, sea urchins were either tethered on open rock surfaces or partially restrained (but untethered) within incomplete cages.

Tethered *C. rodgersii* were exposed on open rock surfaces and monitored individually by a series of 6 tripod-mounted video cameras. Tethering involved drilling two small holes thru the test with a hypodermic needle (100 mm long by 1.25 mm diam.), threading a 150 mm length of monofilament line (0.45 mm diam.) through the needle, and threading a size 1 swivel-clip (8 mm clip gape) and numbered spaghetti tag over the monofilament before the line ends were crimped together with a leader sleeve (size 3). This method results in low mortality (< 5%), and no signs of disease or necrosis were observed around the entry and exit points in the test. Because any mortality usually occurs within 2 days of the operation, tagged animals were monitored for several days and only healthy individuals were used in experiments. Such individuals were clipped to a 2 m length of 6 mm diameter galvanised steel chain anchored across a flat rock platform devoid of crevice refuges for urchins. Two tethering platforms, cleared of macroalgae, were set-up within each MPA with three sea urchins of various sizes (35 – 127 mm test diameter) tethered on each chain. Once the sea urchins were in place, continuous recording commenced with battery changes and diving checks performed daily, and sea urchins replaced as necessary. At MIMR, the video system captured a total of 6 days and nights during April 2004 and May 2005. Due to the close proximity of the CPMR site to laboratory facilities, tethered sea urchins were monitored continuously for 22 days and nights from 5 January 2004 to 2 February 2005.

In addition to video monitoring of tethered *C. rodgersii*, identification of predators preying on untethered, untagged urchins was achieved by constructing an incomplete

cage (with an open ceiling and 300 mm diam. openings in the sides) to partially constrain urchins within camera fields of view while giving full access to potential predators. Video cameras with accompanying infrared lights guarded cage openings and panned the cage interior to maximise detection of predation events. The cage was constructed of 38 mm mesh with a wall height of 1.5 m weighted with chain at the bottom and buoyed with floats at the top, was ~2 m^2 in area, and set up over smooth rock substratum devoid of crevices. Algae and sediment were removed so that sea urchins could successfully attach to the reef substratum via tube feet suctioning. Twenty-eight *C. rodgersii* of a range of sizes (50 – 90 mm TD) were placed in the cage and checked daily, with escapees returned to the cage.

Survival of *Centrostephanus rodgersii* inside and outside no-take MPAs

Predator size and abundance inside and outside MPAs

To test the hypothesis that protected reefs with high predator abundance conferred greater resilience against sea urchin grazing, we assessed predation rates on tethered and tagged (but un-tethered) *C. rodgersii* in MPAs (i.e. unfished reef) and on fished reef. At each experimental reef, the size and abundance of large mobile predatory invertebrates was assessed with 6 belt transects (50 x 4 m), while demersal fishes were surveyed by visual size-graded counts from standardised swims along 6 belt transects (50 x 10 m). Macro-invertebrates were measured in situ using vernier calipers.

Tethering experiment: Predation risk of exposed individuals

Sixteen tethering arrays (each with 3 sea urchins as described above) were arranged at each of two sub-sites within protected (MIMR) and fished reefs in the Mercury Passage. Within a site, sub-sites were 30 x10 m and separated by a distance of 50 m. Swivel-clips and individually numbered spaghetti tags were attached to *C. rodgersii* in two size classes (small 40 - 70 mm TD; large 80 – 120 mm TD). Three urchins were randomly drawn from large catch bags and clipped to the chain anchor at equal spacing ensuring individual urchins could not cluster together (3 urchins by 16 arrays, by 2 sub-sites, by 2 sites giving a total of 192 tethered *C. rodgersii* for the experiment).

Tethered sea urchins were assessed on 9 occasions over a 100 day period by examining each tether array and recording the status of the attached sea urchin as dead or alive. Tethers with missing urchins or the remains of sea urchins attached were recorded as mortality events. Over the duration of the experiment, escapees were recorded as some tethers corroded due to prolonged exposure (17 in MPA; 21 on fished reef). Escapees occurred across all sub-sites and were factored out of the analysis; they were easily identifiable and were readily found sheltering in crevices adjacent to the tethering array.

Tagging experiment: estimates of apparent daily survival and resighting probabilities

To obtain estimates of survival when *C. rodgersii* were able to undergo their normal behaviour, tagged but untethered sea urchins (with tags but no swivel clip; *see above*) were released on reefs inside and outside MPAs and re-surveyed through time. As outlined for tethering above, individuals were held for at least 2 days after tagging, and only healthy urchins were used in the experiment. Tagged individuals displayed normal behaviour, and some individuals tagged during pilot trials retained readable

tags in the field for over 2 years. Multiple re-survey of tagged individuals yielded individual encounter-histories, enabling maximum-likelihood estimation of apparent daily survival and resighting probabilities using a Cormack-Jolly-Seber (CJS) mark-recapture technique (Cormack 1964; Jolly 1965; Seber 1965). At each site, 48 *C. rodgersii* in each of two size classes (small 40 - 70 mm TD; large 80 – 120 mm TD) were placed within crevices (total of 96 sea urchins per site) and monitored through time. Searches for tagged sea urchins were performed across the sites on 8 re-sampling occasions (at 17, 37, 60, 86, 106, 131, and 182 days post release) within a 'census zone' 60 x 10 m at each site. Given high fidelity of *C. rodgersii* for rocky reef crevices, we assumed zero emigration of individuals from the census area and this was supported by a lack of observations of tagged animals outside the census area over the duration of the experiment. The design enabled modelling of the contributions of 'group' (i.e. all combinations of 2 size classes at 4 sites giving n=8 unique groups) and 'time' (i.e. sampling occasions, n=8) to apparent daily survival and resighting probabilities.

Data were analysed using the CJS routine in the MARK® software (White & Burnham 1999), which identifies the most parsimonious CJS model, while excluding parameters that cannot be justified by the data. In this approach there is no null hypothesis or formal test of significance, but rather the concept is one of 'best inference' given the data and a set of *a priori* models (Lebreton et al. 1992). The starting point of the analysis is to confirm that the saturated CJS model (all parameters included) adequately describes variability in the data, i.e. that survival probability (φ) and resighting probability (ρ) depend on both group (g) and time (t), expressed formally as $\varphi(g*t)\rho(g*t)$. Model fit was examined using 1000 bootstraps within the Goodness-Of-Fit (GOF) routine within MARK®.

Size-specific predation dynamics

Physical model

Video footage of spiny lobster (*Jasus edwardsii*) attacks on *C. rodgersii* in the field revealed a highly consistent method of predation. The size of appendages, in particular the span of the first pair of thoracic appendages, appeared important in initiating the attack on sea urchins. On this basis we developed a physically based model assuming that *J. edwardsii* could only predate on *C. rodgersii* if the span (inside circumference) across the first pair of thoracic appendages could extend over the spine canopy (outside circumference) of the sea urchin. The *C. rodgersii* spine canopy was defined as the cross-section circumference determined by spines of average length. The span-width of the first thoracic appendages of lobsters was determined by summing the lengths of each leg segment and the inter-leg distance on the underside of the thorax. Equivalence in the span-width of the first thoracic appendages and urchin spine canopy circumference was used to derive a theoretical upper limit of predation capability on *C. rodgersii* by lobsters of a given carapace length (CL).

Field trials

Video monitoring of tethered *C. rodgersii* allowed estimation of predator size by calibrating the view field. However, because of the potential for sized-based intraspecific competition among spiny lobsters (*J. edwardsii*), which we observed from

the video recordings, an *in situ* caging experiment was employed to give lobsters of a range of sizes sole access to a size range of sea urchins. The caging experiment was conducted within the CPMR from January to February 2005. Cages were constructed from 38 mm mesh and measured 3×3 m with sides 1.5 m tall. The roof and sides were buoyed while the cages were weighted to the reef using 12 mm chain. Cages were bottomless and sealed against the boulder substratum by an inward-folding skirt (150 mm width) weighted by 6 mm chain. Spiny lobsters of 10 different sizes (80, 95, 99, 102, 106, 118, 131, 139, 144 + 153 CL were housed individually in separate cages, and 2 cages containing no predators were assigned as controls. Five *C. rodgersii* (neither tethered nor tagged) from each of three size classes (TD: 40-60 mm, 80–100 mm, and 100 mm+) were placed within each cage. To minimise possible seasonal bias in predation between male and female lobsters, only post-moult *J. edwardsii* were caged in an attempt to maximise feeding motivation. While the cages heavily restricted natural movement of lobsters (which may move 100s m per foraging excursion, H. Pederson *unpub. data*), the 9 m^2 area of each cage ensured densities of both *J. edwardsii* (0.11 m^{-2}) and *C. rodgersii* (1.67 m^{-2}) were within the range of natural densities observed in the field.

To test for possible differences in survivorship of tagged versus untagged *C. rodgersii* an additional cage was deployed to house a single male lobster (163 mm CL) with a total of 42 urchins (ranging from 50-115 mm TD) equally assigned to tagged and untagged treatments. This test was run at CPMR over 2-months from April to May 2005.

Laboratory trials

Given logistical constraints of field experimentation, aquarium trials were also conducted to examine size-specific interactions between lobsters and sea urchins. However, lobsters appeared unmotivated to feed under aquarium conditions and lobsters of a size known to readily attack *C. rodgersii* in the field (from video observations) were generally unmotivated to attack *C. rodgersii* in aquaria even when starved for several weeks (only 2 predation events were observed). In an attempt to ascertain the upper size-limit of predatory interaction, the motivation for attack by lobsters in the aquarium was improved by making a 10 mm diameter puncture through the peristomial membrane of urchins. Sea urchins wounded in this manner were still able to defend themselves with spines, and resisted attack by suctioning to the smooth aquarium surface. Control urchins (50-115 mm TD) injured in this way (n=6) were held in aquaria without predators and were all alive 2 months post injury. Note that *C. rodgersii* with small drill holes in the test, as occurred in the tethering and tagging field experiments, did not elicit consistent attacks from lobsters under aquarium conditions. Aquarium trials involved lobsters across a size range of 72 – 177 mm CL, and sea urchins of 34 – 124 mm TD. For each trial an individual lobster and sea urchin were drawn randomly from holding tanks and put together in a 1,600 L aquarium for a trial period of 2 days and nights, at which point it was recorded whether the sea urchin had been preyed upon. Trials ran from December 2005 to February 2006.

Results

Predatory capability

Remote video monitoring inside MPAs revealed that the spiny lobster, *Jasus edwardsii* (Palinuridae), and the labrid, *Notolabrus tetricus* (Labridae), were capable of predating upon *Centrostephanus rodgersii*. The spiny lobster was chiefly responsible for predation on tethered *C. rodgersii* (Table 1A), and entirely responsible for predation on partially caged (untethered, untagged) *C. rodgersii*, with lobster predation occurring exclusively during night-time (Table 1B). All successful attacks initiated by lobsters on *C. rodgersii* resulted in eventual dislodgement, inversion and consumption of body components via the peristomial region (Figure 2). Furthermore, *J. edwardsii* attacked and successfully consumed all sizes of *C. rodgersii* offered (TD 36 – 127 mm). The labrid was abundant on the experimental reefs and regularly visited the tethering arrays and partial cage during daylight, however attacks by *N. tetricus* were rarely observed in the video monitoring (n=3), with only the smallest tethered *C. rodgersii* attacked (TD < 50 mm, i.e. the size at which *C. rodgersii* is usually cryptic, see Table 1A). Nonetheless, *N. tetricus* displayed a consistent method of attack whereby the labrid (only individuals > 350 mm total fish length) rolled onto its side and used a 'chiselling' motion with its mouth and jaws to wedge beneath the sea urchin and overturn it. With the underside exposed, a swift thrust by the wrasse's jaws to the peristomial region broke apart the test. Internal body components were then completely consumed with only spines and some test fragments remaining.

Table 1. Summary of predator identity and diel timing of predation on *in situ* *Centrostephanus rodgersii* as observed by video monitoring inside MPAs in eastern Tasmania. A. Video monitoring of tethered *C. rodgersii* inside MPAs; predator identity was discernable for a total of 26 predation events observed by monitoring a total of 47 individual sea urchins over a total of 28 days and nights. B. Video monitoring of non-tethered, non-tagged *C. rodgersii* housed in partial cages at the CPMR (December to January 2006); a total of 4 predation events were witnessed over 8 days and nights.

Predator	% of total predation events	
	Diurnal	Nocturnal
A. Tethered *Centrostephanus rodgersii* (N=26)		
Spiny lobster (*Jasus edwardsii*)	0 %	92 %
Blue-throated wrasse (*Notolabrus tetricus*)	8 %	0 %
B. Partially caged *Centrostephanus rodgersii* (N=4)		
Spiny lobster (*Jasus edwardsii*)	0 %	100 %

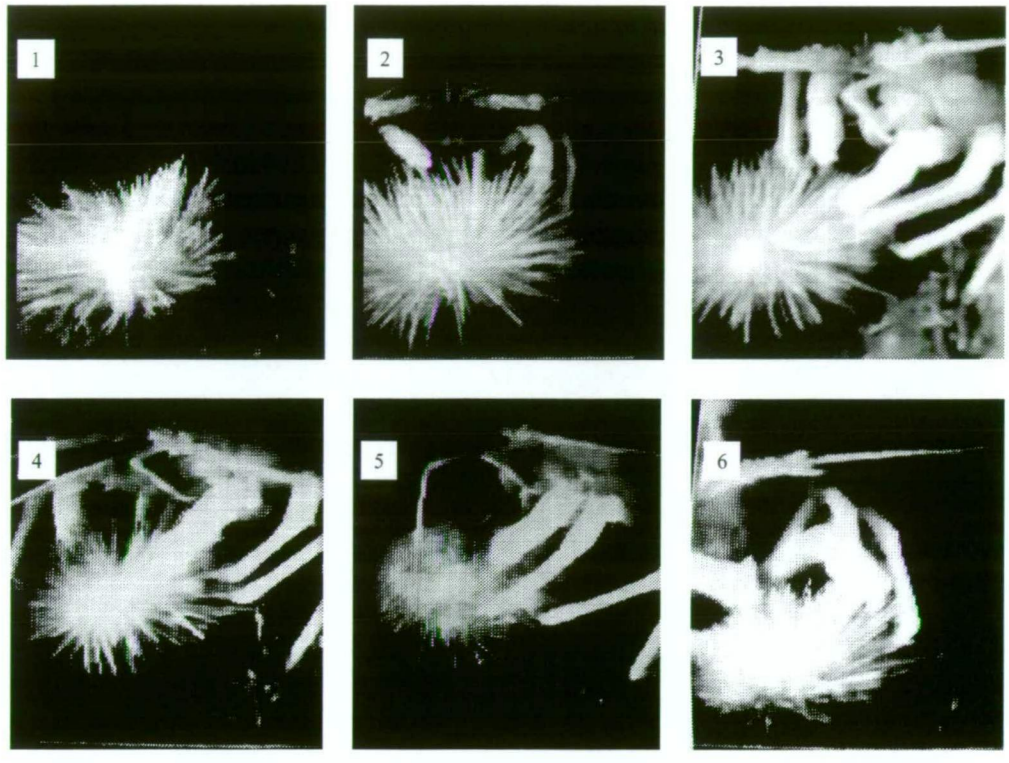

Figure 2. Typical sequence of spiny lobster (*Jasus edwardsii*) predation on *Centrostephanus rodgersii* at night as observed by remote infrared video monitoring inside MPAs. (1) Sea urchin (TD 125 mm) displaying typical relaxed nocturnal spine configuration. (2) Sea urchin displaying antipredator response as evidenced by switch to the defensive spine configuration upon detection of lobster threat. (3) Lobster (160 mm CL) commences to engage sea urchin, (4) successfully grasping and dislodging it before (5) overturning the sea urchin, (6) holding it against the reef substratum dorsal surface down and consuming the urchin through the peristomial opening. Note that the size of the peristomial opening of large *C. rodgersii* allows *J. edwardsii* to access and consume all internal organs without breaking the test. Conversely, tests of small *C. rodgersii* (approximately < 110 mm) were generally fractured from the peristomial region out.

Survival of *Centrostephanus rodgersii* inside and outside no-take MPAs

Predator size and abundance

Assessment of spiny lobster (*J. edwardsii*) size and abundance clearly showed that lobsters inside MPAs are notably more abundant and larger than those on nearby reefs open to lobster fishing (Figure 3). Examination of size and abundance of the protogynous hermaphrodite *N. tetricus* (Labridae) did not reveal clear patterns between experimental reefs inside and outside MPAs, however there was evidence for a slight size bias toward larger terminal phase males inside MPAs (Figure 4). Other demersal carnivorous and/ or omnivorous fishes showed variable patterns of abundance inside and outside MPAs (*see* Appendix II).

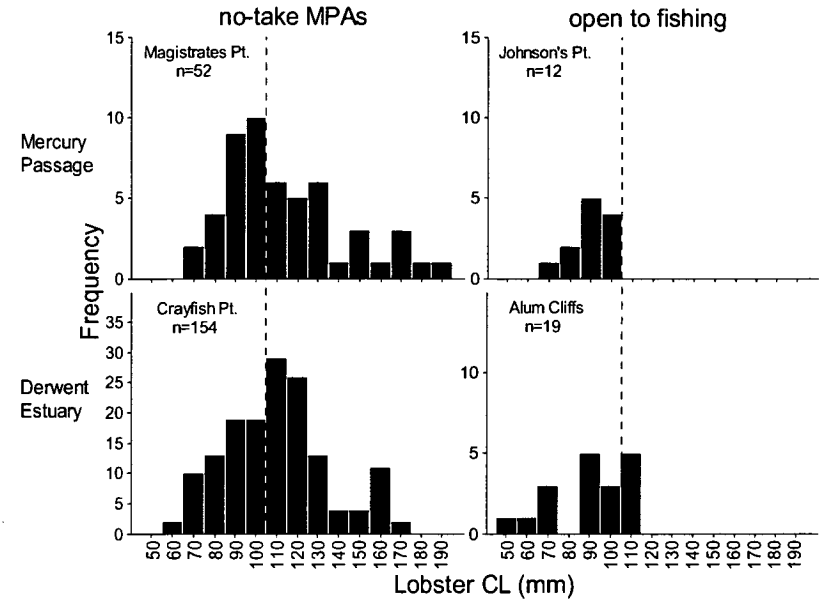

Figure 3. Size and relative abundance of spiny lobsters, *Jasus edwardsii*, at experimental sites inside and outside the MPAs at the two study locations (abundances are per 1200 m^2 of high relief rocky reef). Vertical line represents legal minimum size limit for *J. edwardsii* in Tasmania (minimum legal limit for ♀ =105 mm CL; ♂ =110 mm CL).

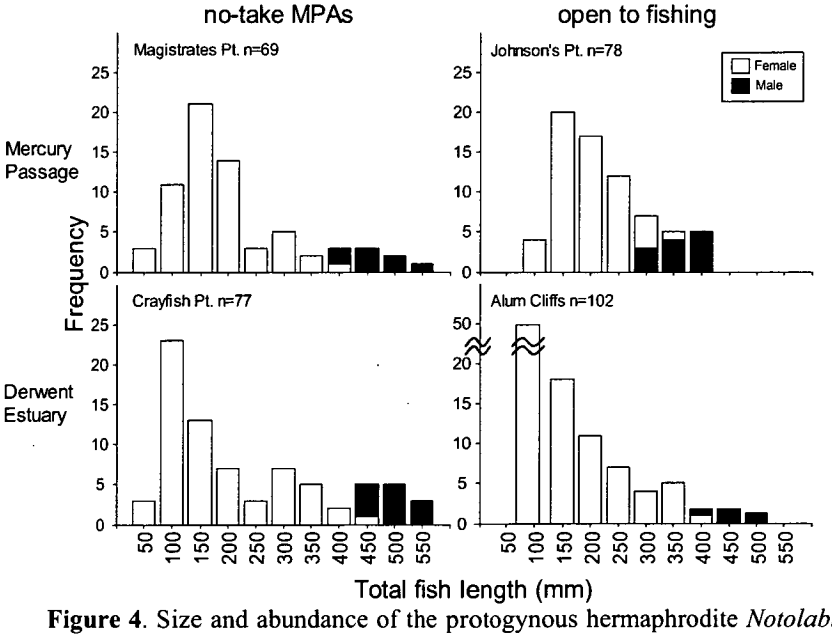

Figure 4. Size and abundance of the protogynous hermaphrodite *Notolabrus tetricus* (Labridae) at experimental sites inside and outside MPAs across the two study locations (abundances are per 3000 m^2 of rocky reef). Note extended scale of y-axis in lower RHS panel and trend towards larger male size inside MPAs.

Tethering experiment: relative survival of exposed Centrostephanus rodgersii

The proportion of tethered *C. rodgersii* surviving through time declined rapidly on protected reef relative to that observed on an adjacent reef open to fishing (Figure 5A). Both small and large tethered *C. rodgersii* showed similar patterns (Figure 5B and 5C). Examination of size-specific survival of tethered *C. rodgersii* inside the MPA reveals a more rapid initial decline of small sea urchins compared with large individuals (cf. Figures 5B, 5C).

Tagging experiment: estimates of apparent survival and resighting probabilities inside and outside MPAs

Multiple re-survey of individually tagged *C. rodgersii* revealed a consistent decline in resighting rates inside MPAs in contrast to a relatively high and stable rate of re-sightings at sites open to fishing (Figure 6). Raw resighting rates at the fished sites stabilised at ~70% of the total tagged urchins released, whereas resighting rates inside the MPAs declined sharply before stabilising at ~25% of the tagged urchins released to the reef. A goodness-of-fit test of the saturated size-specific CJS model indicated satis-

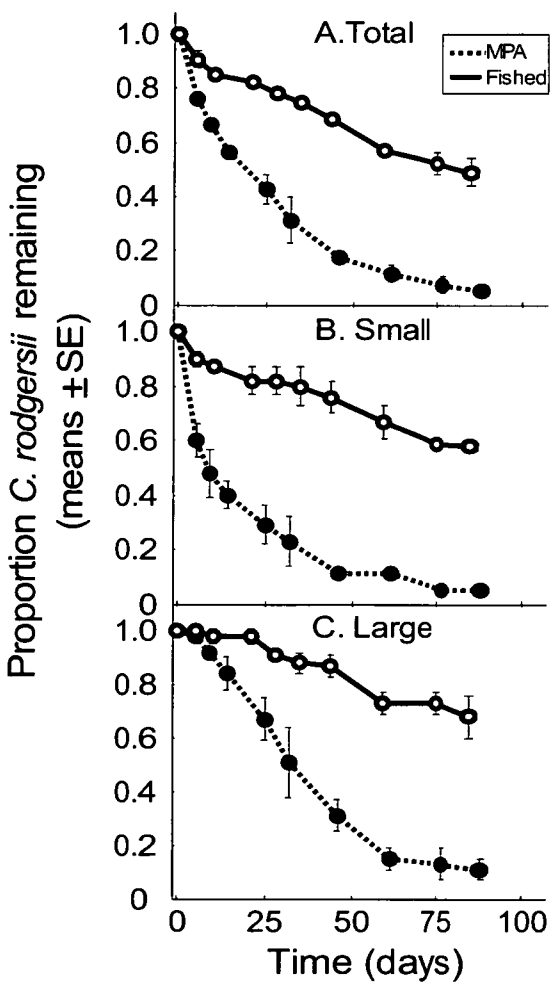

Figure 5. Survival of tethered *Centrostephanus rodgersii* inside (solid symbol, dotted line) and outside (open symbol, solid line) the MIMR. A. Proportion of total sea urchins (small and large) remaining through time, N=48 sea urchins per replicate transect, n=2 replicate transects in MPA and at the fished reef; B. Small sea urchins (40 – 70 mm TD), N=24 sea urchins per replicate transect; C. Large sea urchins (80 – 120 mm TD), N=24 sea urchins per replicate transect.

factory fit (P=0.12), with the model reduction process indicating that the most parsimonious model contained survival and resighting probabilities as a function of experimental 'group' only (i.e. groups based on all combinations of small and large urchins, inside and outside two MPAs) (Table 2).

Estimates of apparent daily survival probability generated by the best supported model revealed reduced survival of *C. rodgersii* inside the MPAs relative to reefs open to fishing (Figure 7A). In addition, estimates of daily resighting probabilities were consistently lower inside the MPAs relative to reefs open to fishing (Figure 7B). For both apparent daily survival and resighting probabilities, significant interaction effects were detected between reef status and sea urchin size, with trends between survival and resighting probabilities negative inside MPAs, but positive for the fished reefs (Figure 7).

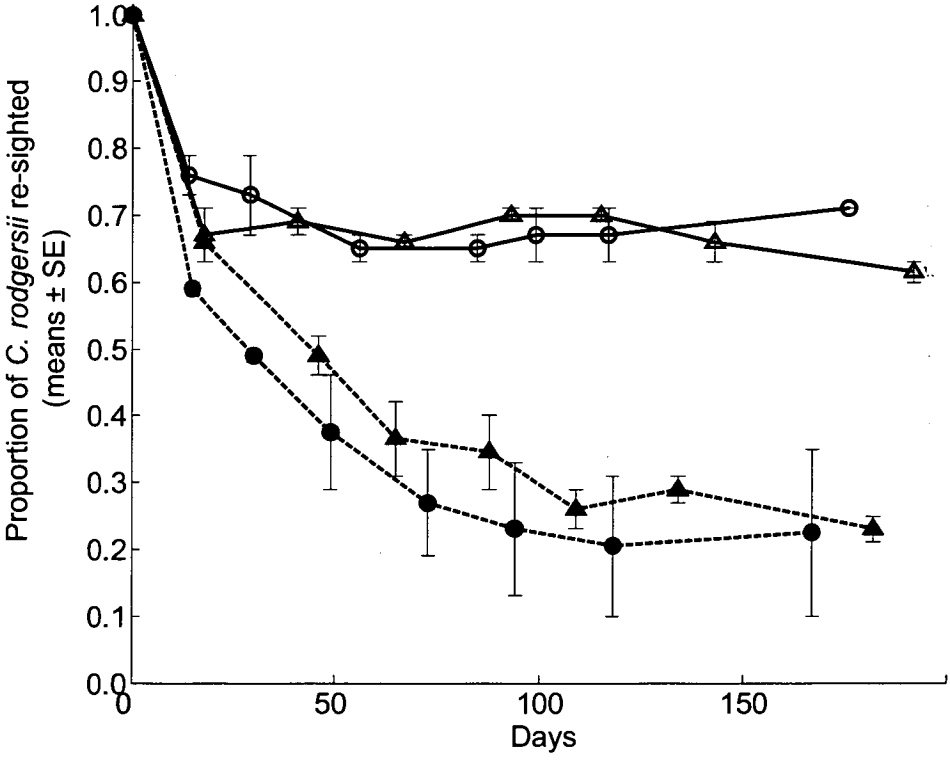

Figure 6. Proportion of tagged *Centrostephanus rodgersii* resighted through time at experimental reefs inside (dotted lines) and outside (solid lines) MPAs. Sites were located in Mercury Passage (Triangles); and the Derwent Estuary (circles).

Table 2. Reduction process for competing Cormack-Jolly-Seber models of apparent survival and resighting probabilities of *Centrostephanus rodgersii* inside and outside MPAs. Survival (φ) and resighting (ρ) probabilities may be a function of experimental 'group' (1-8, i.e. for each combination of small and large urchins at each experimental reef), and or 'time' (sampling occasion 1-8). '*Par*' indicates the number of parameters estimated by each model. Model *AICc* provides a measure of the parsimony of each model [*AICc* = -2log Likelihood + 2*Par* + 2*Par*(*Par* + 1)/(*n* - *Par* - 1), where *n* is the effective sample size]. Competing hypotheses are ordered in terms of the relative weight of evidence in support of a particular model (i.e. *AICc weights*). The saturated model, for which Goodness-of-Fit was performed, is highlighted in bold.

Hypothesis	*Model*	*Par*	*AICc*	*Delta AICc*	*AICc Weight*	*Model Likelihood*	*Deviance*
Survival & sightability both dependent on group	φ (g)ρ(g)	16	3007.7	0.0	1.0	1.0	716.0
Survival dependent on group; sightability dependent on group & time	φ(g)ρ(g*t)	64	3044.5	36.8	0.0	0.0	651.6
Survival dependent on group & time; sightability dependent on group	φ(g*t)ρ(g)	64	3055.1	47.4	0.0	0.0	662.3
Survival dependent on group; sightability dependent on time	φ(g)ρ(t)	15	3063.9	56.2	0.0	0.0	774.2
Survival dependent on time; sightability dependent on group	φ(t)ρ(g)	15	3067.3	59.7	0.0	0.0	777.7
Survival dependent on group; sightability independent of group or time	φ(g)ρ(.)	9	3070.2	62.5	0.0	0.0	792.7
Survival independent of group & time; sightability dependent on group	φ(.)ρ(g)	9	3078.2	70.5	0.0	0.0	800.7
Survival independent of group or time; sightability dependent on group & time	φ(.)ρ(g*t)	57	3102.7	95.0	0.0	0.0	725.0
Survival dependent on time; sightability dependent on group & time	φ(t)ρ(g*t)	62	3103.9	96.2	0.0	0.0	715.4
Saturated model; survival & sightability dependent on group & time	**φ(g*t)ρ(g*t)**	**104**	**3104.7**	**97.0**	**0.0**	**0.0**	**622.6**
Survival dependent on group & time; sightability independent of group & time	φ(g*t)ρ(.)	57	3121.2	113.5	0.0	0.0	743.5
Survival dependent on group & time; sightability dependent on time	φ(g*t)ρ(t)	62	3122.5	114.8	0.0	0.0	734.0
Survival dependent on time; sightability independent of group & time	φ(t)ρ(.)	8	3152.5	144.8	0.0	0.0	877.0
Survival independent of group & time; sightability dependent on time	φ(.)ρ(t)	8	3154.2	146.5	0.0	0.0	878.7
Survival & sightability both dependent on time	φ(t)ρ(t)	13	3158.5	150.8	0.0	0.0	872.9
Survival independent of group or time; sightability independent of group & time	φ(.)ρ(.)	2	3167.9	160.2	0.0	0.0	904.5

Extrapolation of apparent daily survival across one year revealed large separation between hypothetical population projections for *C. rodgersii* inside MPAs relative to fished reefs (Figure 8A). Size-specific projections of urchin populations revealed clear divergence between protected and fished reefs, however there was relatively smaller divergence between projections for small and large urchins within a particular reef status (Figure 8B).

We considered the tagging procedure to have very small, if any, effect on the likelihood of lobster predation which was corroborated by observation that equal numbers of tagged (n=16) and non-tagged urchins (n=16) were consumed when caged with a large predatory lobster in the field over 2 months.

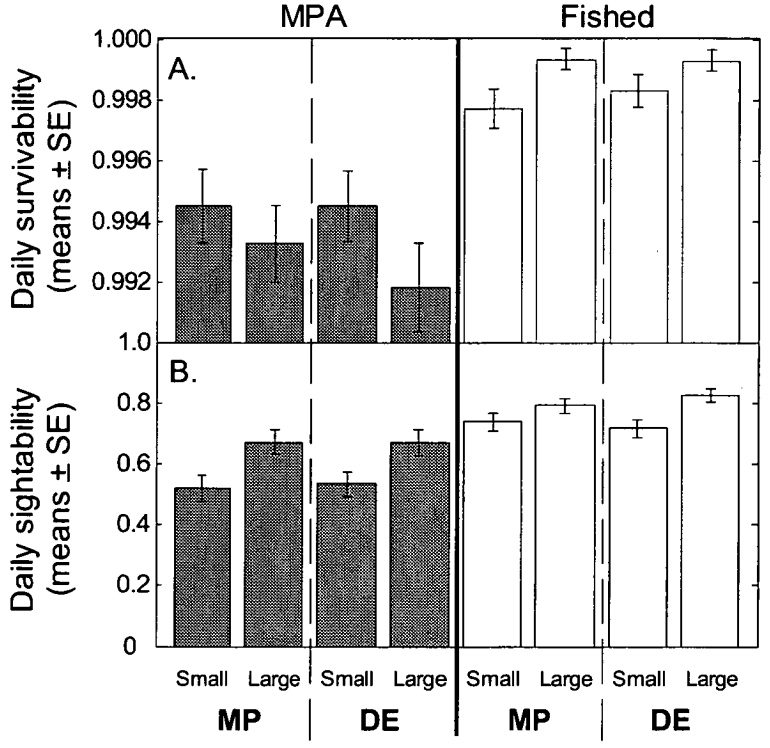

Figure 7. Apparent daily size-specific survival and re-sighting probabilities for *Centrostephanus rodgersii* on experimental reefs inside and outside MPAs as estimated from encounter histories of tagged individuals using the best supported CJS model, i.e. that apparent daily survival and re-sighting probabilities are dependent on experimental group. Size classes of *C. rodgersii* (small = 40 – 70 mm TD; and large = 80 – 120 mm TD) and locations (MP=Mercury Passage; DE=Derwent Estuary) are shown on X-axis. A. Apparent daily survival probability (Model I, 2-way ANOVA on group means, 'MPA', $F_{1,7}$=176.67, P<0.001, 'Size', $F_{1,7}$=0.66, P=0.4607; 'MPA*Size', $F_{1,7}$=18.14, P=0.0131). B. Daily re-sighting probability (Model I, 2-Way ANOVA on group means: 'MPA', $F_{1,7}$=262.46, P<0.0001; 'Size', $F_{1,7}$=116.14, P<0.001; 'MPA*Size', $F_{1,7}$=9.12, P=0.0392).

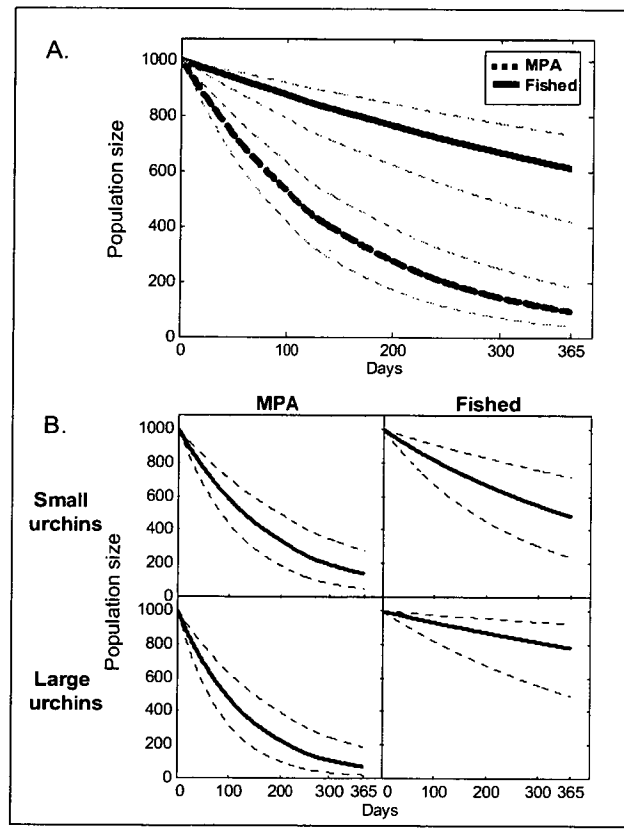

Figure 8. Projection of hypothetical annual population trajectories based on apparent daily survival rate for 1,000 *Centrostephanus rodgersii* 'invading' reef inside and outside MPAs. A. Pooling across size classes. B. Size-specific patterns. Dotted lines indicate upper and lower 95% confidence intervals.

Size-specific predation by lobsters on sea urchins

As revealed from *in situ* video surveillance, lobster size, in particular the span of the first pair of thoracic appendages appeared important in initiating the attack on sea urchins (Figure 9). For lobsters, span-circumference of the first pair of thoracic appendages was linearly related to carapace length (CL) (Figure 10A). For *C. rodgersii*, the relationship between circumference of the spine canopy and test diameter (TD) is described by a logistic curve (Figure 10A). Combining the two relationships, and assuming that the span-circumference of lobsters must be ≥ circumference of the urchin spine canopy, the maximum sized *C. rodgersii* graspable by a lobster followed an exponential relationship (Figure 10B). Overlaying this morphologically based physical model with observed predation events revealed that the upper theoretical limit predicted by the model is in close agreement with the ceiling of observed size-specific predation data (Figure 10B). However, the majority of predation events near the upper 'limit', especially for smaller lobsters (CL <120 mm), were observed in the aquarium experiments. Direct observations in the field estimation via remote video monitoring indicated that indeed only very large "supra-legal" sized lobsters (CL ≥140 mm) were

capable of predating *C. rodgersii* >50 mm TD under natural field conditions (Figure 10B). Examination of apparent daily mortality rate of *C. rodgersii* with respect to the density of supra-legal lobsters revealed evidence for a threshold type response between urchin mortality and the presence of predation capable lobsters (Figure 11A). After correcting for mortality, there was a marked decline in apparent re-sighting probability of the sea urchin in the presence of supra-legal sized lobsters (Figure 11B).

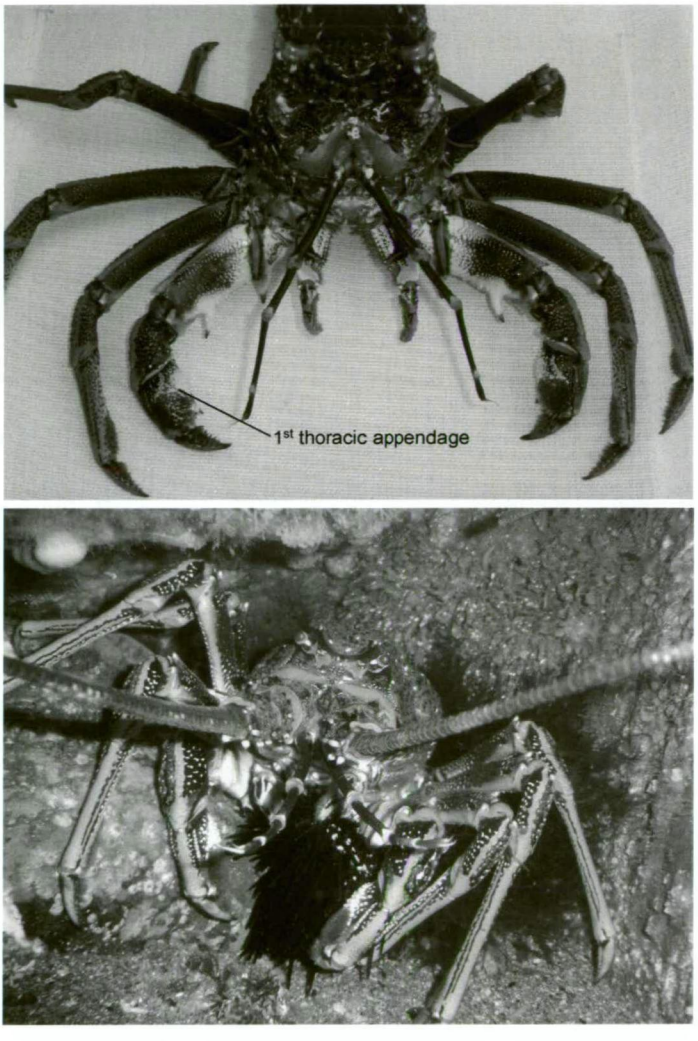

Figure 9. Top panel: anterior view of the spiny lobster *Jasus edwardsii* displaying prominent span-width of the first thoracic appendages considered to be the chief apparatus used to grasp and overturn *Centrostephanus rodgersii*. Lower panel: large *J. edwardsii* (CL 160 mm) in a den consuming a non-tethered, non-tagged *C. rodgersii* (TD 60 mm) captured from the incomplete cage. Note the use of the first thoracic appendages to hold the sea urchin.

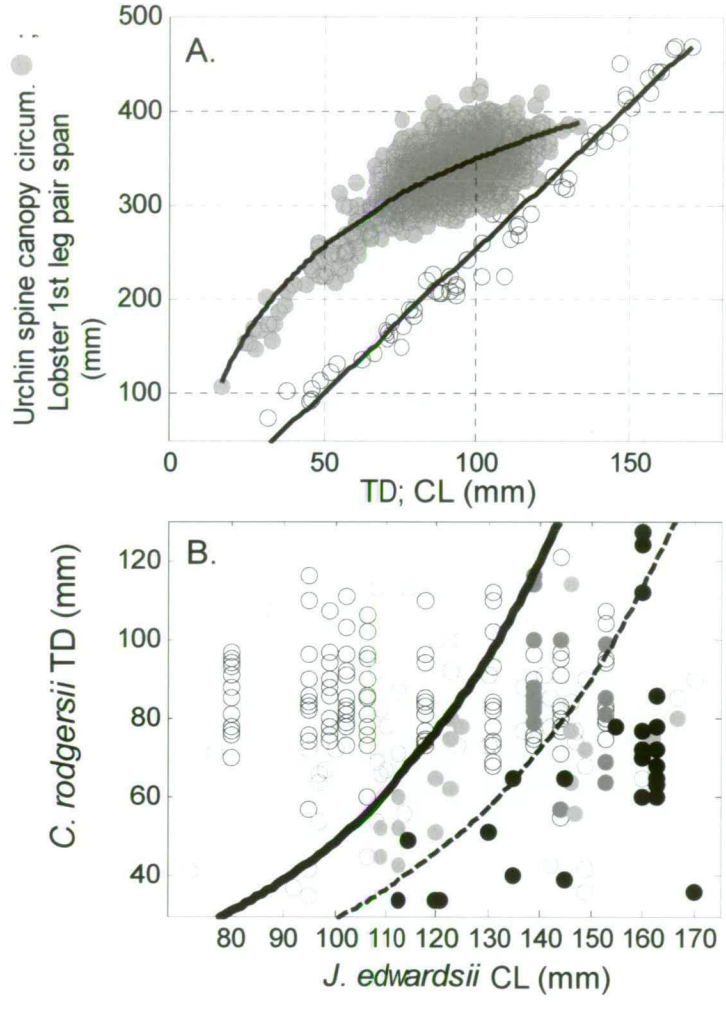

Figure 10. Size-specific predator-prey interaction between lobster *Jasus edwardsii* and sea urchin *Centrostephanus rodgersii*. A. Plot of allometric relationship between span circumference of the first thoracic appendages and carapace length of lobsters (open symbols, trendline y=3.089x-58.68, R^2=0.91, n=71), and the allometric relationship between circumference of spine canopy and test diameter for *C. rodgersii* (filled symbols, trendline y=134.73$Ln(x)$-271.16, R^2=0.62, n=857). B. Physical model (solid line), based on equivalence of lobster span circumference and urchin spine canopy, indicates the theoretical upper limit of size-specific predatory capability of *J. edwardsii* on *C. rodgersii* (y=5.12e$^{0.023x}$), with predation capability to the right of curve only. The model is overlaid with empirical observations of successful predation events (filled circles) and nil-predation events (open circles) obtained from video monitoring (black); *in situ* cages (grey); and aquarium experiments (light grey). Dashed-curve represents 60% of the maximum theoretical size-specific predation curve and approximates the upper predator-prey limit derived from field observations (y=3.08e$^{0.023x}$). Note that minimum legal size of *J. edwardsii* is 105 CL mm ♀ and 110 mm CL ♂; and that the average size of *C. rodgersii* in eastern Tasmania is ~90 mm TD, while size at emergence is ~50 mm TD (Andrew & Byrne 2001).

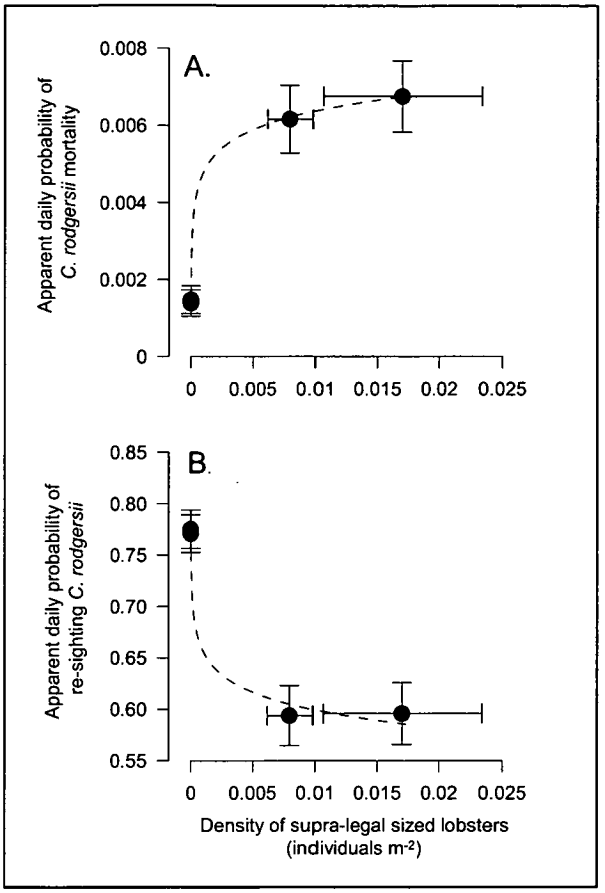

Figure 11. Apparent daily mortality (1-apparent daily survival) (A) and re-sighting probabilities (B) for tagged *Centrostephanus rodgersii* as a function of the abundance of supra-legal sized lobsters (CL ≥140 mm) estimated for experimental sites inside and outside MPAs. Relationships were best described by logarithmic trends (dashed lines) indicating a threshold type response between the presence of supra-legal lobsters and apparent daily mortality, $y=0.0007\text{Ln}(x)+0.01$, $R^2=0.99$; and apparent daily re-sighting rate, $y=-0.0251\text{Ln}(x)+0.48$, $R^2=0.99$; where x=density of supra-legal lobsters and y=mortality and re-sighting probabilities respectively.

Discussion

Temperate rocky reef assemblages are dynamic systems typified by high variability and shaped by interactions between physical and biological processes acting across multiple spatial and temporal scales (e.g. Dayton et al. 1998; Tegner & Dayton 2000; Micheli et al. 2005). While variability typifies these systems, physical and biological perturbations may push ecosystem dynamics beyond a usual range of variability leading to 'catastrophic shifts' in structure and function whereby the underlying dynamic moves to an alternative domain of attraction with return to former dynamics unlikely once a critical threshold is passed (e.g. May 1977; *reviewed by* Scheffer et al.

2001). Recent catastrophic shift from productive kelp beds to sea urchin barrens in eastern Tasmania is the result of overgrazing by the range extending sea urchin *Centrostephanus rodgersii* (Johnson et al. 2005; Ling et al. 2008; Ling 2008). Identifying processes influencing the underlying dynamics of kelp beds, and in particular processes bestowing ecosystem resilience (after Holling 1973) against sea urchin grazing is therefore fundamental to understanding and implementing actions to reduce risk of further catastrophic shifts (e.g. Steneck et al. 2002; Bellwood et al. 2004; Folke et al. 2004; Hughes et al. 2005).

Identification of sea urchin predators within the extended range

The spiny lobster *Jasus edwardsii* (Palinuridae) was observed to be the principal predator capable of attacking and consuming *C. rodgersii* in Tasmania. Importantly, lobster predation occurred on both tethered and untethered urchins (Table 1), but only at night when *C. rodgersii* leaves daytime shelters to graze and is thus graspable by nocturnally foraging lobsters and at risk of being inverted to expose its vulnerable oral surface (Figure 2; also see Tegner & Levin 1983). Attacks on *C. rodgersii* were rarely observed during daylight, with the labrid *Notolabrus tetricus* the only daytime predator. However, only small tethered sea urchins, which usually remain highly cryptic within crevices during daylight, were attacked by *N. tetricus* (Table 1). Thus, strong overlap between the nocturnal foraging behaviour of lobsters and the nocturnal accessibility of *C. rodgersii* identifies lobsters as the predator most capable of successfully preying on this sea urchin within the extended Tasmanian range. Indeed, this finding is consistent with other experimental work where it was also shown that *J. edwardsii* is a more important predator than demersal fishes on the abundant short-spined sea urchin *Heliocidaris erythrogramma* (Echinometridae) in eastern Tasmania (Pederson & Johnson 2006).

In temperate reef systems worldwide, lobsters have been implicated as important predators of sea urchins (clawed lobsters, e.g. Breen & Mann 1976 [Atlantic]; Spiny lobsters, e.g. Tegner & Levin 1983 [California]; Goñi et al. 2001 [Mediterranean]; Mayfield & Branch, 2000 [South Africa]; Shears & Babcock 2002 [New Zealand]; Pederson & Johnson 2006 [Australia]; *also see* Tegner & Dayton 2000). Furthermore, heavy fishing of lobsters has been frequently suggested as being responsible for increases in sea urchin abundance and widespread formation of sea urchin barrens habitat (e.g. Breen & Mann 1976; Tegner & Levin 1983; Shears & Babcock 2002). In the southern hemisphere, protection of rocky reefs from fishing has realised rapid recovery of predators, particularly the spiny lobster *J. edwardsii* (e.g. Edgar & Barrett 1999; Kelly et al. 2000; Shears et al. 2007; *see* Figure 3). Indeed recovery of spiny lobster populations within MPAs has effectively reinstated trophic interactions leading to declines in urchin populations (Babcock et al. 1999; Edgar et al. 2005; Pederson & Johnson 2006; *also see* Mayfield et al. 2001), which in some cases has contributed to shifts from barrens to macroalgal habitat over several decades post cessation of fishing (Shears & Babcock 2002, 2003). The demonstrated predatory capability of large *J. edwardsii* on *C. rodgersii* in eastern Tasmania, and the clear effect of fishing on the individual size and abundance of lobsters on this coast (Edgar & Barrett 1999; Frusher 1997; Figure 3), suggests that by depleting populations of lobsters, fishing increases the risk of *C. rodgersii* establishing in high abundance.

Effect of fishing on sea urchin predation risk

Predation on tethered *C. rodgersii* (exposed on reef surfaces) was 10-times greater on protected reef relative to nearby fished reef (Figure 5). Furthermore, populations of tagged (but untethered) *C. rodgersii*, capable of normal crevice-seeking behaviour, also displayed reduced apparent survival on reefs inside MPAs relative to fished reefs (Figure 7). There results concord with other studies, where sea urchins exposed to high predatory biomass inside MPAs consistently display higher rates of predation risk relative to fished reefs where predator biomass is low (e.g. McClanahan & Muthiga 1989; Sala & Zabala 1996; Shears & Babcock 2002; Guidetti 2006; Pederson & Johnson 2006). Given the overwhelming contribution of spiny lobsters (*J. edwardsii*) to predation of *C. rodgersii* (Table 1), together with the major recovery of lobster abundance, but weaker recovery of demersal fish, inside MPAs (Figure 4; *also see* Barrett et al. 2007), these results indicate that fishing down the biomass of lobsters effectively removes a functional predator and thus reduces predation risk to sea urchins. Reduced predation risk therefore increases the likelihood that sea urchin populations may establish and grow to densities sufficient to effect widespread overgrazing of seaweed habitat (e.g. Breen & Mann 1976; Tegner & Levin 1983; Estes & Duggins 1995; Shears & Babcock 2002, 2003).

Behavioural effects

While predators may influence prey populations directly by increasing prey mortality rates, the indirect effects of predators on prey behaviour is also an important mechanism by which predators may influence the spatial and temporal dynamics of prey populations (*reviewed by* Werner & Peacor 2003). In the presence of predators, sea urchins are widely reported to display diel crypsis (e.g. Nelson & Vance 1979; Bernstein et al. 1981; Cowen 1983; Sala & Zabala 1996; Sala 1997; Sala et al. 1998; Shears & Babcock 2002, 2003; Pederson & Johnson 2006). Consistent with these studies, experimental release of tagged *C. rodgersii* on reef inside and outside MPAs revealed reduced re-sighting of tagged populations on reefs protected from fishing relative to fished reef, suggesting that *C. rodgersii* more often seeks shelter in the presence of predators (Figures 7B & 11B). For sea urchins, mitigating predation risk is chiefly achieved by using the spines to brace the test in crevices and resist attempts at dislodgement, inversion and exposure of the vulnerable spine-free peristomial opening (*see* Figure 2; *also see* Tegner & Dayton 1981; Tegner & Levin 1983; Andrew & Underwood 1989; Andrew 1993; Guidetti & Mori 2005). The ability of *C. rodgersii* to remain cryptic in the day in areas where it can brace in the crevices of complex reef habitat appears an important strategy for minimising predation risk (*see also* Andrew & Byrne 2001).

To effect widespread overgrazing, sea urchins must emerge from the safety of crevices and forage on open rock surfaces. While the predominant mode of formation of *C. rodgersii* barrens hinges on nocturnal grazing sorties from their day time shelters (e.g. Andrew 1993), shelter is not obligatory for *C. rodgersii* to form barrens. Indeed, we have regularly observed widespread barrens occurring on featureless flat-rock habitat where *C. rodgersii* remain fully exposed during the day, with such behaviour typically observable on reefs where the sea urchin occurs at high densities (*see also* Andrew & O'Neill 2000; Andrew & Byrne 2001). Given the apparent predator-driven increase in

cryptic behaviour observed in our experiments (Figure 11B), this result suggests that the presence of predators may indirectly constrain sea urchin grazing to only the most spatially complex reef habitat where individuals may briefly leave crevices to graze but may quickly return to proximal refuge upon threat of predation (e.g. Tegner & Dayton 1981; Cowen 1983; Tegner & Levin 1983; Sala & Zabala 1996; Sala et al. 1998).

If the daytime sheltering behaviour of *C. rodgersii* is driven by the presence of diurnally active fishes, then fish potentially impose an important indirect effect on the sea urchin. The ecological importance of predator induced behaviour in diadematid urchins is suggested by observations by Fricke 1974 (*cited by* Nelson & Vance 1979) who described that grazing by the homing *Diadema setosum*, which demonstrates the usual nocturnal foraging pattern, occurred both night and day when diurnal active predatory fish were locally absent. Indeed, patterns of dispersion, local distribution and nocturnal behaviour of *C. rodgersii* in New South Wales (NSW) have been inferred to be the result of predator avoidance of the diurnal *C. rodgersii* predator *Achoerodus viridis* (Labridae) (*reviewed by* Andrew & Byrne 2001). Note that while *A. viridis* has recently been observed to have extended its range to north eastern Tasmania (S. Ling *pers. obs.*), it only occurs as small individuals and is very rare. Based on the collective evidence, the local presence of predatory capable fishes (day active Labrids), even though appearing to contribute little to *C. rodgersii* predation rates in Tasmania (*see* Table 1), may ultimately exert an important indirect effect on *C. rodgersii* populations by constraining sea urchin foraging to nocturnal periods and necessitating the use of localised crevices for daytime shelter. Thus, the presence of predators would appear to have the potential to restrict grazing activity of *C. rodgersii* to spatially complex reef habitat minimising the extent, persistence and types of habitats on which barrens may form.

Size-dependent patterns in sea urchin predation risk and behaviour

Tethering of both small and large *C. rodgersii* inside MPAs revealed that small urchins (40-70 mm TD) were initially more vulnerable to predation than were larger individuals (80-120 mm TD) (Figure 5B & C). Conversely, when tagged (but untethered) urchins were released onto reefs inside MPAs, and allowed to undergo normal crevice seeking behaviour, the small size class of urchins demonstrated lower re-sighting rates (i.e. greater cryptic behaviour by retreating deeper into crevices) but displayed higher apparent survival relative to large urchins, which were more visible and thus exposed to greater risk of predation (Figure 7). On fished reefs where lobster biomass and therefore predation risk was low, small urchins were also more cryptic than large urchins but here large urchins displayed greater apparent survival than small urchins despite being more exposed on the reef surface. These results clearly indicate that sea urchin predation risk is size dependent and that crevice seeking behaviour is an important means of mitigating predation risk for *C. rodgersii*. Furthermore, this result is highly consistent with work by Pederson and Johnson (2006) who also document a similar pattern of size-based predation risk in the native short-spined Tasmanian sea urchin (*Heliocidaris erythrogramma*). Similar size-dependent patterns in sea urchin survival are reported for other systems where intermediate sized urchins, newly emerged from a cryptic juvenile existence, display greatest predation risk leading to bimodal size distributions of urchin populations in the presence of predators (e.g. Tegner & Dayton 1981; Tegner & Levin 1983; Sala & Zabala 1996; Shears & Babcock

2002; Hereu et al. 2005). Indeed, only large sea urchins with an apparent size refuge have been observed to remain exposed on reef surfaces in the presence of predators (Tegner & Dayton 1981; Cowen 1983; Shears & Babcock 2002; Guidetti 2006).

Size-specific predation capability of lobsters

Protection of rocky reef assemblages from fishing has not only realised rapid escalation of lobster abundance but has also resulted in large increases in the average size of lobsters within protected populations (e.g. Edgar & Barrett 1999; Kelly et al. 2000; Shears et al. 2007; *see* Figure 3). Therefore, in our experiments examining predation risk inside and outside MPAs, it was unclear whether it was the elevated abundance of lobsters or their larger size that was chiefly responsible for increased rates of sea urchin predation inside MPAs (*see* Figures 5&6). Evidence of the size-specific nature of lobster predation was indicated by a more rapid decline of small tethered urchins relative to larger individuals (see size-dependent patterns above), suggesting that the efficiency of lobster predation may decrease with increasing prey size (e.g. Tegner & Levin 1983; Mayfield et al. 2001; Pedersen & Johnson 2006; Langlois et al. 2006).

Revealed by remote video monitoring, the method of lobster attack on *C. rodgersii* was highly consistent (Figure 2). *J. edwardsii* only appeared capable of preying on *C. rodgersii* if the inside circumference of the first pair of thoracic appendages was sufficient to span the spine canopy such that the lobster could grasp and invert the urchin to expose the vulnerable peristomial region. The video footage revealed that lobsters held the sea urchins with their first thoracic appendages while they carried them back to their dens where the urchin was consumed (lower panel, Figure 9). The size-specific predation model, based on the dimensions of the 1st pair of thoracic appendages of the lobster and spine canopy of the sea urchin, revealed close agreement with empirical predation observations and was thus considered a robust descriptor of the upper limit of lobster predation capability on *C. rodgersii* (Figure 10). Importantly, predictions from this model infer that small lobsters, less than the minimum legal carapace length in Tasmania (CL 105 mm females; 110 mm males), essentially have no ability to prey on emergent *C. rodgersii* given that the sea urchin is cryptic below ~50 mm TD (Andrew & Byrne 2001). Therefore even very large populations of sub-legal sized lobsters are unlikely to confer predation risk to *C. rodgersii*, particularly where reef habitat is complex and provides an abundance of crevices for juvenile sea urchins to remain cryptic (*see also* Shears and Babcock 2003; Hereu et al. 2005; Pederson & Johnson 2006). Because the average size of emergent *C. rodgersii* in eastern Tasmania is ~90 mm TD (S. Ling *unpublished data*), based on predictions of the physical model the minimum size of lobster capable of successfully preying on these urchins is ~130 mm CL. Considering that predators are observed to generally target prey at approximately 60% of the maximum prey size consumable (*see* Mumby et al. 2006), this would require a lobster of approximately ≥140 mm carapace length to be an efficient predator of *C. rodgersii* under natural conditions. Indeed, this estimate is supported by field experiments in which direct observations of predation (from remote video monitoring) revealed that only lobsters of ~140 mm CL and larger preyed on *C. rodgersii* under natural conditions.

Consistent with our results, Pederson and Johnson (2006) demonstrate that large *J. edwardsii* are capable of preying on a broad size-range of the sea urchin *Heliocidaris*

erythrogramma. These authors also found that sub-legal sized lobsters were unable to predate on larger individuals of *H. erythrogramma*. On other coasts, work in North America (Tegner & Levin 1983), South Africa (Mayfield et al. 2001) and New Zealand (Andrew & MacDiarmid 1991) has similarly demonstrated the size-specific nature of predatory interactions between palinurid lobsters and sea urchins. Similar sized-based shifts in dietary breadth are also documented for labrids (e.g. Cowen 1983; Gillanders 1995), and while we observed very few predation events by *N. tetricus*, all involved large fish (> 350 mm length). Therefore, in the presence of large predators typical of protected reefs, sea urchin populations will experience predation mortality over a greater portion of their life span relative to fished reefs where average predator size is small and where urchins obtain a size refuge at a relatively smaller size (e.g. Cowen 1983; Tegner & Levin 1983; McClanahan & Muthiga 1989; Shears & Babcock 2002, 2003; Pederson & Johnson 2006).

Historical effects of fishing on the resilience of kelp beds

Projections from stock assessment models have estimated that the biomass of legal-sized rock lobsters (CL ≥105 mm ♀; 110 mm ♂) on the east coast of Tasmania has recently been as low as 2–8 % of the virgin stock depending on location (Frusher 1997). Clearly demonstrating the effect of fishing on the size and abundance of lobsters, protection of reefs in eastern Tasmania has realised rapid recovery of lobster biomass, particularly of the supra-legal size class (Edgar & Barrett 1999; Edgar et al. 2005; *see* Figure 3). Size frequency data pre- and post-fishing in eastern Tasmania similarly indicates that fishing, has significantly reduced the average size of *J. edwardsii*, and has particularly reduced the abundance of supra-legal individuals (≥140 mm CL) (Figure 12). Similarly, in New Zealand, documentation of commercial landings of *J. edwardsii* from virgin offshore reef show that lobsters caught in the first year of fishing averaged ~160 mm CL for males and ~130 mm CL for females (Kensler 1969).

Evidence from other temperate coasts also indicates that fishing has greatly reduced the individual size of spiny lobsters. In California the average size of the spiny lobster *Panulirus interruptus* pre-industrial fishing is estimated to be ~150 mm CL (Dayton et al. 1998). By calculating carapace length from mandibles preserved in South African middens, the average size of *Jasus lalandii* prior to industrialised fishing in this region is also estimated to be much larger than presently seen in modern fished populations (A. Jerardino *pers.comm.*). Given the strong size-specific nature of predation capability by lobsters (Figure 10), the trophic potential of spiny lobster populations has clearly been modified by fishing (*also see* Tegner & Levin 1983; Dayton et al. 1998; Shears & Babcock 2002). The overwhelming contribution of supra-legal lobsters to sea urchin mortality in our study, and rare predation by a single species of fish, strongly suggests that diversity within the urchin predator guild is very low in eastern Tasmania (*see* Steneck et al. 2002; Bellwood et al. 2004; Micheli & Halpern 2005). However, notwithstanding such low trophic diversity, the resilience of kelp beds in eastern Tasmania is likely maximised by the presence of an entire assemblage of large predatory capable lobsters and fishes to effectively maximise overall predation risk and behavioural constraints on sea urchins.

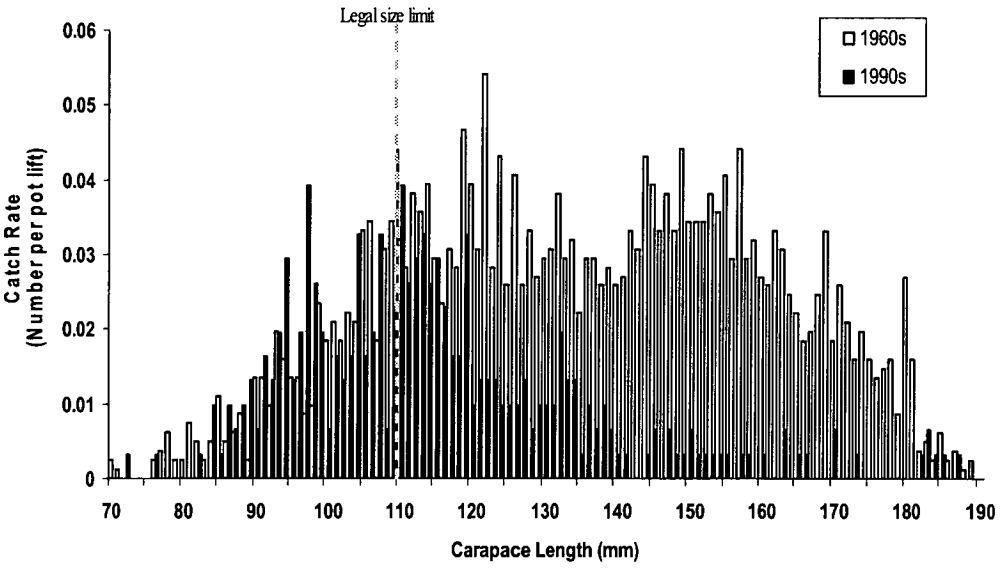

Figure 12. Historical change in size-frequency of *Jasus edwardsii* in eastern Tasmania. Data are for the remote Flinders Island, far north eastern Tasmania (data redrawn from Frusher 1997).

Conclusions

Our experimental results demonstrate clearly that only supra-legal sized spiny lobsters are capable of predating on *C. rodgersii* under field conditions. We therefore infer that removal of a large biomass of supra-legal sized lobsters by fishing has effectively reduced the resilience of kelp-dominated reefs against establishment of this range extending sea urchin, and ultimately increased the risk of catastrophic shift to widespread barrens. Management aimed toward re-building resilience of kelp beds by increasing the abundance of supra-legal sized predators will have the effect of reducing the risk of further catastrophic grazing by *C. rodgersii* in the face of a warming climate. These results provide overwhelming support for the concept of resilience and non-equilibrium dynamics as a useful conceptual framework for understanding marine ecosystems.

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CHAPTER 7. GENERAL DISCUSSION: OVERFISHING REDUCES ECOSYSTEM RESILIENCE AGAINST CLIMATE CHANGE CATASTROPHE

Abstract

Recent catastrophic shift from productive seaweed beds to barrens habitat in eastern Tasmania has been caused by climate-driven range expansion of the sea urchin *Centrostephanus rodgersii* (Diadematidae). Given current population trends and future climate change projections for the region, there is strong likelihood of further barrens formation with concomitant loss of important ecosystem services. Coincident with formation of *C. rodgersii* barrens in the extended range is heavy fishing of reef predators. We identify large "supra-legal" spiny lobsters (*Jasus edwardsii* - Palinuridae) as the chief sea urchin predator. Fishing has drastically reduced the abundance of large lobsters and comparisons inside and outside no-take marine protected areas revealed reduced survivorship of *C. rodgersii* in the presence of large predatory lobsters. We demonstrate that fishing, by removing large lobsters, has reduced the resilience of seaweed dominated systems and increased the risk of catastrophic barrens formation in the face of climate warming.

Introduction, results, discussion

Modern context for marine ecosystems

Globally, ecosystems are being increasingly perturbed by human activity (e.g. Vitousek et al. 1997). Ecosystems appear able to absorb some level of stress but catastrophic-shifts in structure and function can occur, with a return to former states unlikely, once a critical stress-threshold is passed (e.g. Holling 1973; May 1977; *reviewed by* Scheffer et al. 2001). Importantly, ecosystems are rarely perturbed by one form of stress alone with the total magnitude of perturbation on an ecosystem often the result of multiple stressors acting synergistically (e.g. Beisner et al 2003). The modern context for marine ecosystems involves changing climate (Meehl et al. 2007), overfishing (e.g. Jackson et al. 2001; Pitcher et al. 2001; Myers & Worm 2003), habitat loss (e.g. Pandolfi et al. 2003; Pyke 2004), invasive species (e.g. Carlton & Geller 1993; Lodge 1993) and pollutants (e.g. Fleeger et al. 2003; Islam & Tanaka 2004). With increasing intensity and frequency of multiple stressors, there is an urgent need for marine ecologists to understand ecosystem properties in order to curb trajectories of catastrophic ecosystem change and loss of important ecosystem services (e.g. Folke et al. 2004; Hughes et al. 2003, 2005; Scheffer et al. 2001).

Incursion of *Centrostephanus rodgersii* in Tasmania – warming climate

One of the most commonly observed shifts in shallow sub-tidal temperate marine systems is the transition from productive seaweed beds to sea urchin 'barrens' habitat as a result of overgrazing by sea urchins (*reviewed by* Pinnegar et al. 2000; Steneck et al. 2002). In the Australian context, no other benthic herbivore has as large a role in determining the state of shallow reef communities as the long-spined diadematid sea urchin *Centrostephanus rodgersii* (Agassiz) (Andrew & Byrne 2001). Such is the ecological importance of this sea urchin that in central and southern New South Wales (NSW) this species maintains barrens on approximately half of all near-shore rocky reef (Andrew and O'Neill 2000).

Driven by a changing regional climate, *C. rodgersii* has recently undergone southward range extension to eastern Tasmania (Figure 1a; *see* Chapters 2 & 3) where it has commenced overgrazing of seaweed beds leading to an impoverished and unproductive barrens state (Johnson et al. 2005; *see* Chapter 4). Consistent with the fingerprint of climate change (Parmesan & Yohe 2003), long-term change to the East Australian Current (EAC) has resulted in greater poleward (southward) penetration of warm water leading to warming of coastal waters in eastern Tasmania (Ridgway 2007; *see* Figure 1a). This warming corroborates with poleward range extensions of many marine species to eastern Tasmania (e.g. Edgar 1999; Poloczanska et al. 2007), including *C. rodgersii* which has demonstrated a gradual poleward incursion indicated by the timeline of discovery along the coast (Figure 1a), and a pattern of decreasing age with latitude (Figure 1b; *see* Chapter 3). Importantly, the sea urchin displays high reproductive potential and is capable of producing viable larvae across its extended range, with the warming waters of eastern Tasmania becoming increasingly favourable for successful larval development (Figure 1c; Chapter 2). Given predictions of continued warming for this coast (e.g. Cai et al. 2005; Poloczanska et al. 2007), the likelihood of further population expansion of *C. rodgersii* and associated ecosystem impacts appears high (Chapter 3).

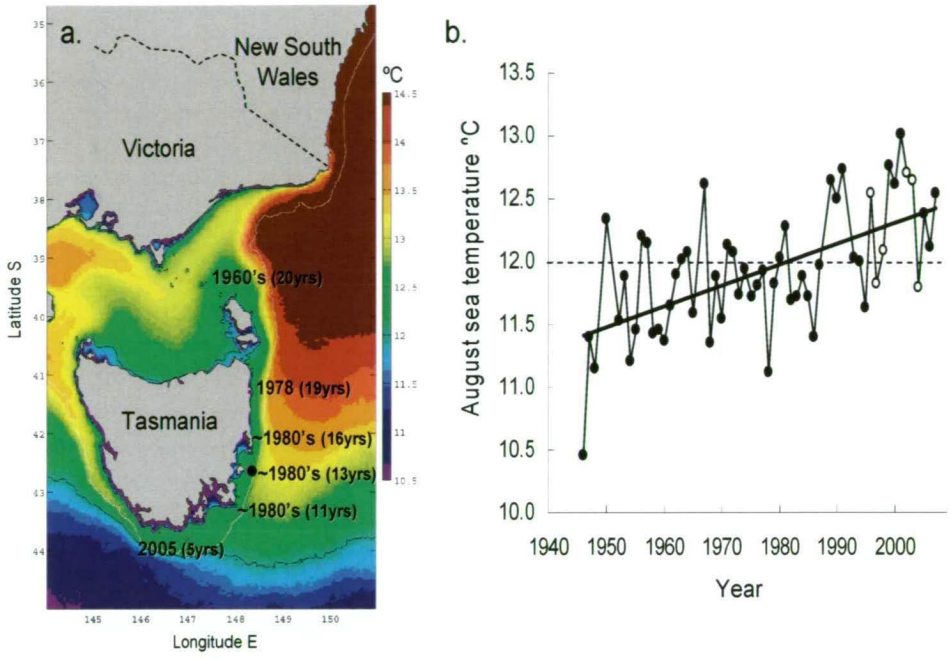

Figure 1. Recent climate-driven range extension of *Centrostephanus rodgersii* to eastern Tasmania. (a) Map of south eastern Australia showing influence of the warm East Australian Current in eastern Tasmania during Austral winter (June-August averaged for the period 1993-2007). Year of first discovery of *C. rodgersii* and mean population ages (in parentheses) are displayed along the coast (*see* Chapter 3). (b) Long-term winter warming trend of coastal waters in eastern Tasmania, 1946-2007 (courtesy of CSIRO Marine & Atmospheric Research), *see* Chapter 2. Data are mean sea temperatures from the Maria Island coastal station, solid point in (a), for August (i.e. the month of major spawning for *C. rodgersii* in Tasmania); dashed horizontal line indicates the 12 °C larval development threshold for *C. rodgersii* (Chapter 2). Note that open symbols represent robust satellite derived estimates of sea surface temperature at the long-term station for recent years with missing *in situ* data (*after* Ridgway 2007).

Formation of sea urchin barrens habitat

The transition from seaweed beds to *C. rodgersii* barrens provides an example of a classic 'catastrophic shift' between alternative and stable reef states with a strong hysteresis effect, i.e. return to the seaweed-dominated state requires reducing sea urchin densities to much lower levels than the threshold at which destructive overgrazing occurred in the first place (Andrew & Underwood 1993; Figure 2; *see* Chapter 1). Given strong negative effects on local biodiversity (Chapter 4) and reef based fisheries (Andrew & Underwood 1992; Johnson et al. 2005), and given the possibility that barrens in eastern Tasmania could in time occur at the same scale as currently observed in NSW (Johnson et al. 2005); barrens formation by this sea urchin poses a major threat to biodiversity and the fisheries dependent on the macroalgal dominated reef systems of eastern Tasmania.

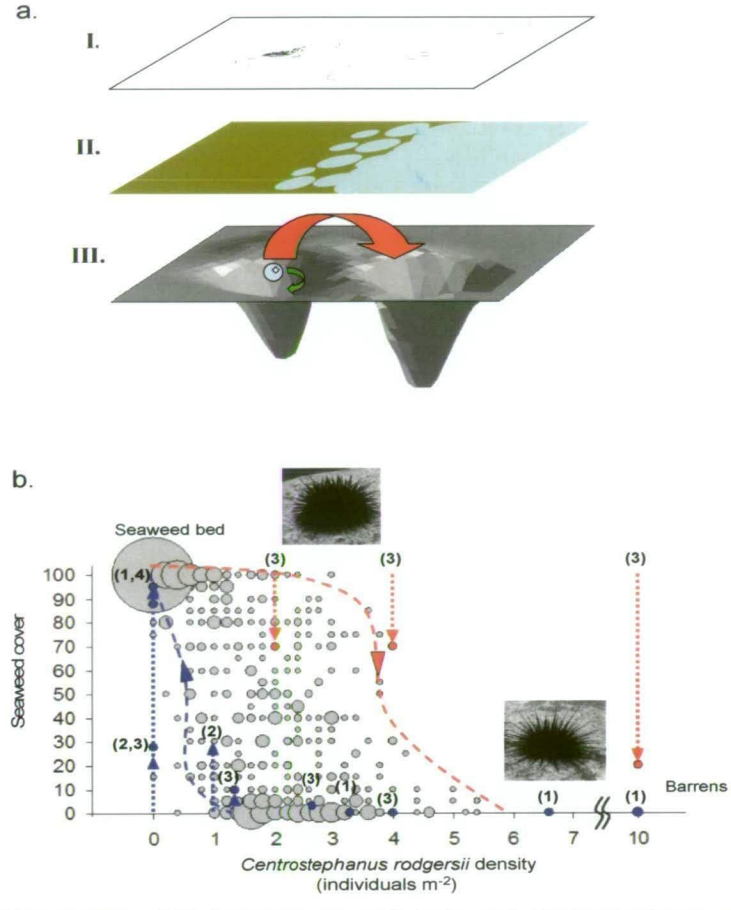

Figure 2. Catastrophic shift between seaweed beds and *Centrostephanus rodgersii* barrens. (aI) Ordination plot (nMDS, stress=0.10) showing alternative community states: seaweed assemblage encompassed by ellipse on LHS, barrens RHS (from Chapter 4); (aII) Schematic landscape view of barrens formation, *C. rodgersii* forms small grazed patches within seaweed beds with catastrophic shift to widespread barrens habitat occurring when grazed patches coalesce; (aIII) schematic conceptualisation display of alternative "domains of attraction" for the seaweed and barrens states; position of the ball represents current ecosystem status, and to shift to barrens the system must be perturbed sufficiently for the ball to roll from one domain of attraction to another. (b) Bubble plot of seaweed cover versus sea urchin abundance for eastern Tasmania. Bubbles represent relative frequency of particular urchin density and seaweed cover combinations as measured in 575 individual 5 m^2 plots (data for 415 plots from Johnson et al. 2005). Arrows and numbers in parentheses indicate magnitude and direction of ecosystem response to: removals of *C. rodgersii* from barrens in NSW after 18 mths, Andrew 1991[(1)], Andrew & Underwood 1993[(2)], ~5 months Hill et al. 2003[(3)], and Tasmania after 18 mths [(4)] (*see* Chapter 4); plus additions of *C. rodgersii* to seaweed beds after ~5 months Hill et al. 2003[(3)]. Dashed red curve represents theoretical 'forward-shift' path from seaweed dominated to barrens dominated states; dashed blue curve represents theoretical 'reverse-shift path from barrens back to the seaweed dominated state (*after* Scheffer et al. 2001). Data between 'forward' and 'reverse' shift paths represent the region of instability. Images of *C. rodgersii* showing alternative morphologies associated with seaweed-beds (short-spines) and barrens (long-spines).

Superimposed on the climate-driven incursion of *C. rodgersii* to eastern Tasmania is heavy exploitation of rocky reefs (e.g. Frusher 1997; Chapter 6). Long-term changes to reef species inside Marine Protected Areas (MPAs) relative to adjacent fished sites show that fishing has a major impact on the abundance and size structure of major target species (Edgar & Barrett 1999). Most striking is the recovery of the spiny lobster *Jasus edwardsii* (Palinuridae) inside marine reserves, where the abundance and size structure of this benthic predator demonstrates rapid recuperation following protection from fishing (Edgar & Barrett 1999; Edgar et al. 2005). Indeed, only large individuals of this lobster are known to be effective natural predators of sea urchins (Andrew & MacDiarmid 1991; Babcock et al. 1999; Shears & Babcock 2003; Pederson & Johnson 2006). Importantly, fishing is estimated to have reduced the stock of legal-sized lobsters on eastern Tasmanian reefs to 2-8% of virgin biomass (Frusher 1997). However, it was unknown whether *J. edwardsii*, or any other reef predators in Tasmania, were capable of preying upon the large and long-spined *C. rodgersii*. Remote video surveillance of tethered and partially caged *C. rodgersii* inside no-take MPAs revealed that large supra-legal sized lobsters (carapace length $\geq$ 140 mm) were the principal predators capable of preying upon this sea urchin (Figure 3a, *see* Chapter 6).

Isolating the exact mechanism(s) underpinning the shift from seaweed beds to sea urchin barrens has long intrigued marine ecologists. While few generalities can be made across systems, and despite lack of critical evidence for particular systems, a consistent unifying theme is that barrens-habitat arises in areas where sea urchin predators are heavily fished, i.e. the 'top-down' consumer control paradigm (*reviewed by* Steneck 1998; Pinnegar et al. 2000; Tegner & Dayton 2000; Steneck et al. 2002; Halpern et al. 2006). Given the global perspective, and evidence in Tasmania of reduced abundances of spiny lobsters as a result of fishing (Frusher 1997; Edgar & Barrett 1999), it was important to assess whether fishing has reduced seaweed bed resilience and thus increased the risk of catastrophic overgrazing by *C. rodgersii* (i.e. 'forward-shift' in Figure 2b) given the climate-driven incursion of this sea urchin to eastern Tasmania (Chapter 2 & 3).

Spiny lobsters and seaweed bed resilience

To examine the influence of fishing on seaweed bed resilience, we translocated large numbers of individually tagged *C. rodgersii* to reefs inside no-take MPAs (i.e. high abundance of large lobsters) and to adjacent reefs open to fishing (few large lobsters) to simulate invasion of Tasmanian reefs by the sea urchin. The no-take MPAs spanned two regions in eastern Tasmania, Maria Island Marine Reserve (MIMR - est. 1992, 12 yrs protection at time of experiment); and Crayfish Point Research Reserve (CPMR - est. 1971, 33 yrs protection at time of experiment) (Chapter 6). Placed within rocky crevice shelters, individually tagged *C. rodgersii* remained localised on the experimental reefs and were surveyed on 8 occasions at various intervals over ~180 days. Consistent with observations of high rates of predation by large lobsters on tethered urchins inside MPAs, the percentage of tagged urchins re-sighted alive declined rapidly inside MPAs compared with resighting rates on adjacent fished reefs (Figure 3b; *see* Chapter 6). Estimation of apparent daily survival rates calculated using

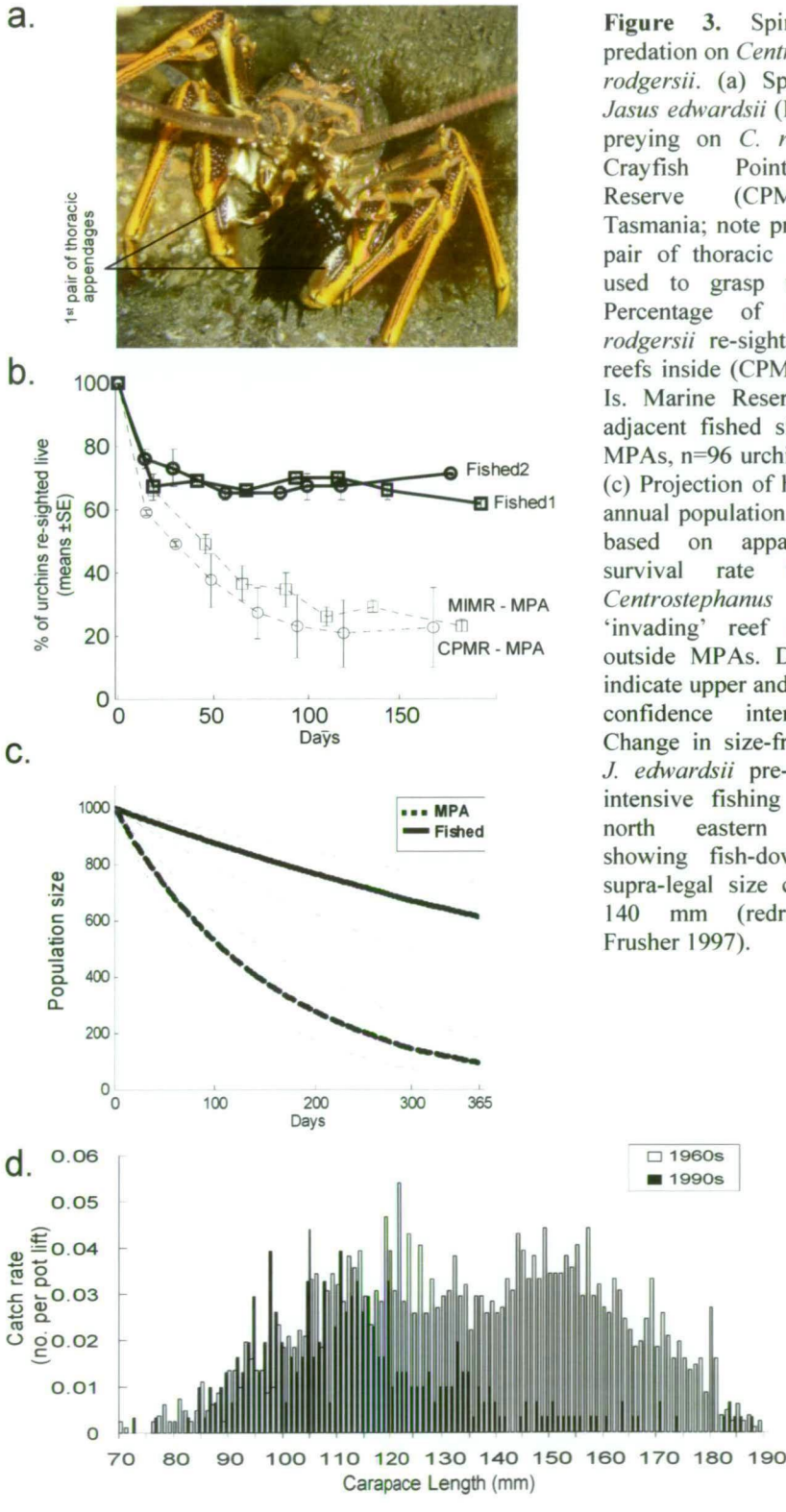

Figure 3. Spiny lobster predation on *Centrostephanus rodgersii*. (a) Spiny lobster *Jasus edwardsii* (Palinuridae) preying on *C. rodgersii* at Crayfish Point Marine Reserve (CPMR), SE Tasmania; note prominent 1st pair of thoracic appendages used to grasp urchin. (b) Percentage of tagged *C. rodgersii* re-sighted alive at reefs inside (CPMR & Maria Is. Marine Reserve) and at adjacent fished sites outside MPAs, n=96 urchins per reef. (c) Projection of hypothetical annual population trajectories based on apparent daily survival rate for 1,000 *Centrostephanus rodgersii* 'invading' reef inside and outside MPAs. Dotted lines indicate upper and lower 95% confidence intervals. (d). Change in size-frequency of *J. edwardsii* pre- and post-intensive fishing in remote north eastern Tasmania showing fish-down of the supra-legal size class CL ≥ 140 mm (redrawn from Frusher 1997).

the Cormack-Jolly-Seber (CJS) method (using program MARK®, White & Burnham 1999) revealed significantly reduced survival rates of tagged *C. rodgersii* inside MPAs relative to the fished reefs (Figure 3c, *see* Chapter 6). Furthermore, after factoring for survival, sea urchins inside MPAs were more cryptic on the reef suggesting modification of behaviour in the presence of predators (*see* Chapter 6). These data strongly indicate that the presence of large predatory capable "supra-legal" lobsters (CL >140 mm) can have a negative effect on the invasion success of *C. rodgersii*. As evidenced from recovery of lobster size-structure inside MPAs (Edgar & Barrett 1999; Edgar et al. 2005; *see* Chapter 6) and catch data from eastern Tasmania, fishing has clearly reduced the abundance of large lobsters on this coast (Figure 3d). Combined, these results strongly suggest that fishing, by removing large lobsters, equates to a reduction in seaweed bed resilience and therefore increased risk of catastrophic overgrazing by *C. rodgersii* in the face of warming climate (Figure 4). While *C. rodgersii* has initiated catastrophic overgrazing of seaweed beds at many sites in eastern Tasmania (Johnson et al. 2005) the large majority of rocky reef remains in the desirable, albeit low resilience (i.e. heavily fished), seaweed-dominated state. Management should focus on preventing further catastrophic-shift because the strong hysteresis effect makes rehabilitation of existing barrens back to seaweed beds exceedingly difficult (*see* 'reverse-shift' Figure 1, Andrew & Underwood 1993).

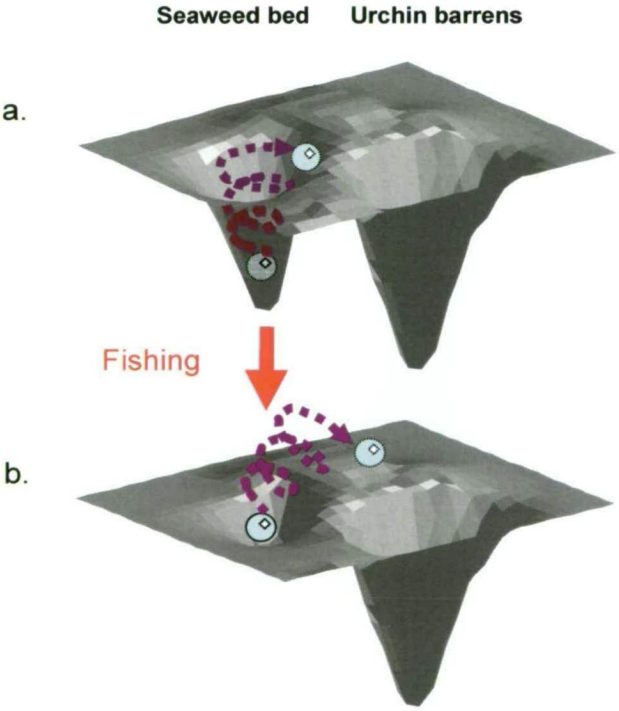

Figure 4. Conceptualisation of loss of seaweed-bed resilience due to fishing large lobsters and associated increase in risk of catastrophic shift to the alternative *Centrostephanus rodgersii* barrens state. (a) Pre-fished seaweed bed with high abundance of large predatory lobsters and high resilience (indicated by basin depth). (b) Heavily fished seaweed-beds with shallow 'basin' and thus lower resilience. Helical line represents perturbation of the seaweed system in the form of climate-driven incursion of *C. rodgersii*. The likelihood of catastrophic-shift to sea urchin barrens depends on the size of the perturbation, same in both (a) & (b), and the basin depth, i.e. "resilience" (after Holling 1973) of the seaweed-dominated state.

To demonstrate the hysteresis effect, take for example, a starting sea urchin density of 2 m^{-2} and assume strict adherence to the barrens formation ('forward-shift') and seaweed recovery ('reverse-shift') paths. In the seaweed dominated state, and following the 'forward-shift' (upper path), urchin density must increase form 2 m^{-2} to ~2.2 m^{-2} (an increase of 0.2 m^{-2}) for the system to catastrophically-shift to the barrens state. Alternatively, assuming the same starting density of urchins in the barrens state, and following the seaweed recovery ('reverse-shift') path, urchin density must decrease from 2 m^{-2} to approximately <1 m^{-2} for the system to return to the desired seaweed dominated state. Thus, approximately 5 times as much predation would be required to revert barrens to seaweed beds as that required to maintain the seaweed dominated state by keeping urchin density just below the 'forward-shift' threshold for barrens formation. Furthermore, *C. rodgersii* on widespread barrens appear less vulnerable to predation as such individuals possess relatively long and more protective spines compared to individuals observed within seaweed habitat where spines are frequently eroded by whiplash of robust seaweeds under the influence of ocean surge (Figure 2b; *see* Chapter 5).

Conclusions

Our data strongly suggest that re-building the abundance of supra-legal lobsters in seaweed beds provides an important management opportunity to increase ecosystem resilience and thus reduce likelihood of widespread overgrazing given the climate associated sea urchin perturbation (Figure 4). By capturing the uncertain nature of rocky reef ecosystem dynamics within broad "domains of attraction", this conceptualisation is not constrained by the traditional equilibrium based paradigms of either 'top-down' or 'bottom-up' control. Rather, as theorised by others (Hughes et al. 2005; Scheffer et al. 2005), this novel approach encompasses multiple processes across a broad range of spatial and temporal scales and incorporates the role of history, and non-equilibrial dynamics in the tempo and mode of ecosystem change. In demonstrating the applicability of this concept to a temperate reef system, this example vindicates the adoption of resilience based ecosystem management focussed on reducing the likelihood of catastrophic ecosystem change, particularly in the face of rapidly changing climate and unprecedented levels of predator removal from the world's oceans.

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Appendix I. List of taxa recorded for barrens, recovered and intact macroalgal patches, 'X' indicates presence of taxa.

Phylum	Species/ Taxa	Incipient barrens	Recovered macroalgal bed	Intact macroalgal bed
Chlorophyta	*Apjohnia laetevirens*	-	X	X
	Chaetomorpha coliformis	X	-	X
	Cladophora fereydayi	X	X	-
	Codium fragile	-	X	-
	Filamentous green	X	-	-
Phaeophyta	*Acrocarpia paniculata*	-	-	X
	Carpomitra costata	-	X	X
	Colpomenia peregrina	X	-	-
	Cystophora retroflexa	-	X	-
	Dictyota dichotoma	X	X	X
	Ecklonia radiata	X	X	X
	Halopteris paniculata	-	X	-
	Phyllospora comosa	X	X	X
	Sargassum paradoxum	-	X	-
	Sargassum vestitum	-	X	-
	Undaria pinnatifida	-	X	-
	Xiphophora gladiata	-	X	-
	Zonaria/ Lobophora complex	X	X	X
Rhodophyta	*Ballia caltricha*	-	X	X
	Callophyllus lambertii	-	X	-
	Ceramium excellens	-	X	-
	Champia viridis	-	-	X
	Curdiea angustatum	-	X	X
	Delisea pulchra	-	X	-
	Encrusting coralline	X	X	X
	Filamentous red	X	-	-
	Haliptilon roseum	-	X	X
	Jeanerita lobata	-	X	X
	Kallymenia sp.	-	X	X
	Lenomandia marginata	-	X	X
	Peyssonelia sp. (prostrate)	X	X	X
	Phacellocarpus pepperocarpus	-	X	X
	Plocamium angustatum	-	X	X
	Plocamium mertensii	-	X	X
	Polyopes constrictus	X	X	X
	Ptereocladia capillacea	-	X	-
	Halicnide similans	-	-	X
	Rhodoglossum sp.	-	X	-
	Rhodymenia sp. 1	X	X	X
	Rhodymenia sp. 2	-	X	X
	Rhodymenia sp. 3	-	X	X
	Rhodymenia? Sonderi	-	X	X
	Sonderapelta coriacea	-	X	X
	Stenogramme interrupta	-	X	X
	Thamnoclamnium dichotomum	-	-	X
Porifera	*? Leucosolenia sp.*	-	X	X
	encrusting sponge	X	X	X
	erect sponge sp. 1	-	-	X
	erect sponge sp. 2	-	X	X
Cnidaria	*Phlyctenactis tuberculosa*	-	X	-
	Phlyctenanthus australis	-	X	X
	Polyp A	-	X	X
	Polyp B	-	X	-
	Gymnagium ascidies	-	X	-
Platyhelminthes	*Platyhelminth sp.*	-	-	X
Nemertea	*Nematerean sp.*	-	X	X
Nematoda	*Nematode sp.*	X	X	X
Annelida	? polychaete	-	X	X
	Chrysopetalid polychaete sp. 1	-	-	X
	Chrysopetalid polychaete sp. 2	-	X	X
	Chrysopetalid polychaete sp. 3	-	X	-
	Chrysopetalid polychaete sp. 4	-	X	-
	Chrysopetalid polychaete sp. 5	-	X	-
	Eunice polychaete sp. 1	-	X	X

Phylum	Species/ Taxa	Incipient barrens	Recovered macroalgal bed	Intact macroalgal bed
Annelida con't	*Eunice polychaete sp. 2*	-	X	X
	Eupolymnia koorangia	-	-	X
	Galeolaria caespitosa	X	X	X
	Hirudinea sp. 1	X	-	X
	Hirudinea sp. 2	-	X	X
	Maldanid polychaete sp. 1	-	X	X
	Maldanid polychaete sp. 2	-	-	X
	Nereid polychaete sp. 1	-	X	X
	Nereid polychaete sp. 2	-	X	X
	Nereid polychaete sp. 3	-	X	X
	Nereid polychaete sp. 4	-	X	X
	Oligochaete sp. 1	-	X	X
	Oligochaete sp. 2	-	X	-
	Phyllodosid polychaete sp. 1	-	X	-
	Phyllodosid polychaete sp. 2	-	X	X
	Sabellid polychaete	-	X	X
	Serpulid polychaete	-	X	X
	Syllid polychaete sp. 1	-	X	X
	Syllid polychaete sp. 2	X	X	X
	Syllid polychaete sp. 3	-	X	X
	Syllid polychaete sp. 4	-	X	X
	Syllid polychaete sp. 5	-	X	-
	Syllid polychaete sp. 6	-	X	X
	Syllid polychaete sp. 7	-	X	X
	Syllid polychaete sp. 8	-	X	-
	Syllid polychaete sp. 9	-	X	X
	Syllid polychaete sp. 10	-	X	X
	Terebellid polychaete	-	X	X
	Turretilid polychaete sp.1	-	X	X
	Turretilid polychaete sp.2	-	X	X
Sipuncula	*Sipunculid sp.*	-	X	X
	Phascolosoma sp.	-	X	-
Arthropoda	*Pallenopsis gippslandie*	-	X	X
	Pseudopalene ambigua	-	X	X
	Pseudopalene sp. 2	-	X	-
	Pseudopalene sp. 3	-	X	X
	Stylopalene longicaudata	-	X	X
	Pyncnigonad sp.	X	-	X
	Syllid polychaete sp. 2	X	X	X
	Syllid polychaete sp. 3	-	X	X
	Syllid polychaete sp. 4	-	X	X
	Syllid polychaete sp. 5	-	X	-
	Syllid polychaete sp. 6	-	X	X
	Syllid polychaete sp. 7	-	X	X
	Syllid polychaete sp. 8	-	X	-
	Syllid polychaete sp. 9	-	X	X
	Syllid polychaete sp. 10	-	X	X
	Terebellid polychaete	-	X	X
	Turretilid polychaete sp.1	-	X	X
	Turretilid polychaete sp.2	-	X	X
	Balanus trigonus	X	X	X
	Lepadomorph cirriped	-	X	X
	Calanoid copepod	-	X	X
	Harpacticoid copepod	X	X	X
	Ostracod sp. 1	X	X	X
	Ostracod sp. 2	-	-	X
	Nebalia sp.	X	-	-
	Leptocuma sp.1	X	X	X
	Leptocuma sp.2	-	X	X
	Apseudes tanaid sp. 1	-	X	X
	Apseudes tanaid sp. 2	-	X	-
	Tanaid sp.	-	X	X
	Leptochelia tanaid	-	X	X
	Nototanaid	-	X	X
	Zeuxo tanaid	-	X	X
	Mysid	X	X	X
	Idoteid isopod	-	X	X

Phylum	Species/ Taxa	Incipient barrens	Recovered macroalgal bed	Intact macroalgal bed
Arthropoda con't	*Sphaeromatid isopod sp. 1*	-	X	X
	Sphaeromatid isopod sp. 2	-	-	X
	Sphaeromatid isopod sp. 3	-	X	-
	Sphaeromatid isopod sp. 4	-	X	X
	Sphaeromatid isopod sp. 5	-	X	X
	Sphaeromatid isopod sp. 6	-	X	-
	Sphaeromatid isopod sp. 7	X	X	X
	Sphaeromatid isopod sp. 8	-	X	-
	Sphaeromatid isopod sp. 9	-	X	X
	Gnathid isopod sp. 1	-	X	X
	Gnathid isopod sp. 2	-	X	X
	Gnathid isopod sp. 3	-	X	X
	Gnathid isopod sp. 4	-	-	X
	Astacillid isopod	-	X	X
	Janirid isopod	-	X	X
	Valviferran isopod	-	X	X
	Anthurid isopod	-	X	X
	Limnorid isopod	-	X	X
	Caprella amphipod sp. 1	X	X	X
	Caprella amphipod sp. 2	X	X	X
	Caprella amphipod sp. 3	-	X	X
	Caprella amphipod sp. 4	-	-	X
	Caprella amphipod sp. 5	X	X	X
	Philantid amphipod	-	X	-
	Ampithoid amphipod	-	X	X
	Corophid amphipod sp. 1	X	X	X
	Corophid amphipod sp. 2	-	X	X
	Deximinid amphipod sp. 1	-	X	X
	Deximinid amphipod sp. 2	-	X	X
	Deximinid amphipod sp. 3	-	X	X
	Deximinid amphipod sp. 4	-	X	-
	Deximinid amphipod sp. 5	X	X	X
	Isaeid amphipod sp. 1	X	X	X
	Isaeid amphipod sp. 2	X	X	X
	Isaeid amphipod sp. 3	-	X	X
	Jaeropsid amphipod	-	X	X
	Jaredopsis amphipod	X	-	-
	Leucothoid amphipod sp. 1	X	-	-
	Leucothoid amphipod sp. 2	-	X	-
	Lyssianossid amphipod	X	X	X
	Podocerid amphipod sp. 1	X	X	X
	Podocerid amphipod sp. 2	X	X	X
	Podocerid amphipod sp. 3	-	X	X
	Podocerid amphipod sp. 4	-	X	X
	Eusirid amphipod	-	-	X
	Austrophenoides amphipod sp. 1	X	X	X
	Austrophenoides amphipod sp. 2	-	X	X
	Austrophenoides amphipod sp. 3	-	-	X
	Rhynchocinetes kuiteri	X	X	X
	Hippolyte australiensis	-	X	X
	Alpheid decapod sp.	X	X	X
	Striopagurus strigmatus	-	X	-
	Paguristes handreckii	X	X	X
	Paguristes squamosus	X	X	X
	Leptomithrax majid sp. 1	X	X	X
	Leptomithrax majid sp. 2	-	-	X
	Notomithrax sp.	-	X	X
	Actaea peronii	-	X	-
	Nectocarcinus tuberculata	X	X	X
	Nectorcarcinus sp.	-	X	-
	Plagusia chabrus	-	X	X
Mollusca	*Lorica volvox*	X	X	X
	Acanthochitonidae polypl. sp. 1	-	X	X
	Acanthochitonidae sp. 2	-	X	X
	Fissurellidae sp. 1	X	X	X
	Fissurellidae sp. 2	-	-	X
	Australium squaliferum	X	X	X

Phylum	Species/ Taxa	Incipient barrens	Recovered macroalgal bed	Intact macroalgal bed
Mollusca con't	*Callistoma armitilla*	-	X	X
	Phasianella australis	-	X	-
	Phasianella ventricosa	X	X	X
	Phasianotrochus eximus	-	X	X
	Phasianotrochus rutilus	-	X	X
	Hypertrochus monachis	-	X	X
	Pyramidellid gastropod sp.	-	X	X
	Maoriculpus roseus	-	X	X
	Turritilid gastropod sp. 1	-	X	X
	Turritilid gastropod sp. 2	-	X	-
	Turritilid gastropod sp. 3	-	-	1
	Pseudobittium?	X	X	X
	Pseudobittium sp. 1	-	X	X
	Pseudobittium sp. 2	-	-	X
	Turbinid gastropod sp. 1	X	X	X
	Turbinid gastropod sp. 2	-	X	X
	Turbinid gastropod sp. 3	-	X	X
	Cymatiid gastropod sp. 1	-	X	-
	Cymatiid gastropod sp. 2	-	X	X
	Cymatiid gastropod sp. 3	-	X	X
	Cymatiid gastropod sp. 4	-	X	X
	Cymatiid gastropod sp. 5	-	X	X
	Trochid gastropod sp.	-	X	X
	Turbo undulatus	-	X	X
	Cabestana spenglerii	X	X	X
	Cymatiid gastropod sp. 6	X	-	-
	Cymatiid gastropod sp. 7	-	X	-
	Sassia verrucosa	-	X	X
	Agwenia tritoniformis	-	X	-
	Columbellid gastropod	-	X	-
	Volumetrid gastropod	-	X	-
	Volutid gastropod	-	X	-
	Marginellid gastropod	-	X	X
	Zafra atkinsoni	-	X	X
	Haliotid sp.	-	X	X
	Cassidae sp.	-	X	-
	Mitrid gastropod	-	-	X
	Fasciolariid gastropod	-	-	X
	Aplysia opisthobranch gastropod	-	-	X
	Actaeonid gastropod	-	X	X
	Dorid gastropod	-	X	X
	Chromodorid gastropod 1	-	X	X
	Chromodorid gastropod 2	-	-	X
	Chromodorid gastropod 3	-	-	X
	Chromodorid gastropod 4	-	-	X
	Mytilid bivalve sp. 1	X	X	X
	Mytilid bivalve sp. 2	X	X	X
	Mytilid bivalve sp. 3	-	X	X
	Musculoides bivalve sp. 1	-	X	X
	Musculoides bivalve sp. 2	-	X	-
	Chlamys asperrimus	-	X	X
	Cleidothaerus albidus	-	X	X
	Lima sp.	-	X	X
	Lasea australis	-	X	X
	Barnea sp.	X	X	X
	Octopus warringa	-	X	-
	Brachiopod sp.	X	X	X
	Bryzoa sp. 1	-	X	X
	Bryzoa sp. 2	-	X	X
	Bugula sp.	-	X	X
Brachiopoda	*Cornucopia grandis*	-	X	X
Bryzoa	*Orthoscutella ventricosa*	-	X	X
	Triphyllozoon umbonatum	-	X	X
	Heliocidaris erythrogramma	X	X	X
	Temnopleurid echinoid	-	X	X

Phylum	Species/ Taxa	Incipient barrens	Recovered macroalgal bed	Intact macroalgal bed
Mollusca con't	*Holopneustes inflatus*	-	X	-
	Holuthurian sp. 2	-	X	-
	Gorgonocephalid sp.	-	X	X
Echinodermata	*Antedon loveni*	-	X	X
	Cenolia tasmaniae	X	X	X
	Cenolia trichoptera	X	X	X
	Asterid asteroid sp.1	-	X	-
	Asterid asteroid sp.2	-	X	-
	Asterinid asteroid	-	X	X
	Asteroid sp. 1	-	X	-
	Asteroid sp. 2	-	X	-
	Ophactis australis	-	X	-
	Ophactis resiliens	X	X	X
	Ophactis sp.	-	-	-
	Ophiothrix sp.	-	X	X
	Amphipholis squamata	-	X	X
	Centrostephanus rodgersii	X	-	-
Chordata	*Pyura australis*	-	X	X
	Ascidian solitary sp. 2	-	X	X
	Ascidian colonial	-	-	X
	Ascidian solitary sp. 3	-	X	-
	Okipleura sp.	-	X	-
	Clinid sp. 1	-	X	-
	Clinid sp. 2	-	X	-
	Perciformes sp.	-	X	-
	Scorpaenid sp.	-	-	X
	Sygnathid sp. 1	-	-	X
	Sygnathid sp. 2	-	X	-
	Gobiescocid sp.	-	X	X
	Aspagomaster sp.	-	X	X

Appendix II. Density of demersal carnivorous and omnivorous fishes (other than *Notolabrus tetricus*) inside and outside MPAs at Mercury Passage (top panel) and Derwent Estuary (lower panel) as assessed by dive transects 10 x 50 m (n=6). The total density of demersal carnivorous/ omnivorous fishes (including *N. tetricus*) inside MPAs was 19.25 individuals 500 m^{-2} (± 4.58 SE), compared to 23.83 individuals 500 m^{-2} (± 5.83 SE) at the fished sites.